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THE VALUE OF THE STUDY OF MITOCHONDRIA IN CELLULAR PATHOLOGY[1]

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THE problem is a wide one, because it has been shown conclusively in the past few years that mitochondria are almost though not quite coextensive in distribution with living protoplasm. They have attracted the attention of botanists, zoologists, anatomists, physiologists, pathologists and clinicians, who have all studied them from varied points of view. A conservative estimate would place the bibliography of the last decade at about 600 papers, scattered widely in the journals of all countries.[2] Any account of the results obtained and the outlook for further investigation is bound to be somewhat narrow and one-sided. A botanist might emphasize the mitochondrial origin of plastids, base thereon the thesis that without mitochondria it is questionable whether we could have any green plants, and go on to philosophise about all life being dependent upon mitochondria. A zoologist would, in all likelihood, devote considerable time to a discussion of the behavior of mitochondria in the developing egg and sperm, their rôle in fertilization and histogenesis, and the possibility that they may be concerned in the hereditary transmission of certain characteristics.

[1] Annual Samuel G. Gross Lecture of the Philadelphia Pathological Society, 1923.

[2] Reviews: Duesberg, J., Ergebn. d. Anat. u. Entwicklungs.-gesch., *20*, 567–916, 1912. Benda, C., Verhandl. d. deutsch. path. Gesellsch., 5–42, 1914. Cowdry, E. V., Section on Mitochondria in a Text-book of General Cytology to be published by the University of Chicago Press, April, 1924.

A physiologist would stress the undoubted but obscure relation of mitochondria to cellular activity. Each specialist would certainly have his own distinctive reaction, so that the best that I can hope to do is hurriedly and incompletely to review the subject as it appeals to an anatomist keenly interested in pathology. As a background for discussion it may be helpful to mention briefly certain properties of mitochondria which have been definitely established.

(1) *Occurrence.* In bacteria it is very questionable whether mitochondria exist, although they have been described by Alexeieff[3] and granules may be observed in some of the larger forms which stain more or less specifically with janus green. They have, however, been repeatedly found in the algae and fungi and in a very primitive group called mycetozoa, since its members partake of the properties of both plants and animals. Thus far they have been reported with but few exceptions in all the higher forms of both kingdoms which have been adequately studied. In their breadth of distribution they rival the nucleus. They are present in embryos, in the young, in adults and in the aged. But it is recognized that in the terminal stages of cytomorphosis, when the cells are actually moribund, they tend to disappear, as, for instance, in non-nucleated red blood cells and desquamating epidermal cells. It is worthy of note that in the life cycle of erythrocytes they persist for an appreciable time after the loss of the nuclei. An interesting parallel may be drawn between the behavior of mitochondria during the formation of hemoglobin in animals and the development of chlorophyll in plants. In both cases, with the aging of the cell, there is a disappearance of mitochondria and the formation of pigment.

Now that the first flush and excitement of discovery are past, we may, in the natural course of events, expect a little retrenchment from unqualified statements to the effect that mitochondria occur in *all* cells. In other

[3] Alexeieff, A., C. rend. Soc. de Biol., *89*, 728–730, 1923.

words, it is probable that lowly plants and animals—and also certain tissue cells of higher forms—will soon be reported in which mitochondria do not occur or in which the materials said to represent them differ so widely from the typical mitochondria of vertebrates that the term can not rightly be applied to them. For example, among the protozoa, the paraplasms pass through a stage of development within the red blood corpuscles of vertebrates in which the cytoplasm is very much reduced, and *anaplasma marginale* (the parasite of East Coast Fever) is said during this phase to consist wholly of nuclear material.[4] It would be a crucial test to ascertain whether with an increase of cytoplasm mitochondria appear, because, if so, it would be a clear case of their *de novo* origin.

(2) *Morphology.* Throughout the length and breadth of the world of living things, wherever they occur, the morphology of mitochondria is remarkably uniform. Comparing again the two great divisions of nature, we find a similar range of variation in the shape of mitochondria in animals and plants.[5] Indeed, it would be a difficult task to find any other cellular component which is so nearly identical in the two. Passing to mammalian and human tissues, which interest us more directly, we observe that different cells are fitted to perform their duties with mitochondria of more or less distinctive shape. Thus, a marked difference is noticeable in the various categories of human blood cells. They tend to be unusually filamentous in gland cells, in nerve cells and in tissues of the developing embryos of all vertebrates. Although their length varies from say 0.5 to 10 microns and their diameter from about 0.5 to 1 micron, their girth in the cells of the same tissue is astonishingly uniform. From this we assume that interactions between the cytoplasm and the mitochondria can only profitably

[4] Theiler, Sir Arnold, 1910. "Texasfieber, Rotwasser und Gallenkrankheit der Rinder." Zeitschr. f. Infektionskrankheiten der Haustiere, *8*, 39; Velu, H., 1922. "Les piroplasmes et les piroplasmoses." Paris, E. Larose, 285 pp.

[5] Cowdry, N. H., *Biol. Bull.*, *33*, 196–228, 1917.

take place in a certain thickness of mitochondrial substance, so that we have two attributes—length and breadth—independently variable and probably influenced by different factors.

(3) *Arrangement.* Within individual cells, mitochondria are usually distributed without definite order throughout the cytoplasm, but some interesting exceptions are to be noted. In the parotid they are clumped in the proximal pole; in intestinal epithelial cells at both poles; and in the thyroid of the opossum, according to Bensley,[6] in the distal cytoplasm. So that there is some reason to believe that they may act as indicators of secretory polarity, like the Golgi apparatus.

Perinuclear condensations of mitochondria have been observed repeatedly in both plants and animals. To illustrate, we may refer to the early meristem in which no definite arrangement is noticeable while in the older cells mitochondria come into actual contact with the nucleus, where they enlarge to form plastids, which finally migrate away from the nucleus and become more or less evenly distributed in the surrounding cytoplasm. This migration has been noted repeatedly by botanists who have detected a coincident increase in their resistance to the solvent action of acetic acid. Similarly, in the spermatogonia of certain animals the mitochondria make their way to the nucleus and become so closely applied to it that some investigators have been led to think that they actually originate from it. In the later stages of spermatogenesis they leave the vicinity of the nucleus and become more resistant to acetic acid. Actual movements to and fro have been observed by W. H. and M. R. Lewis[7] in living tissue cultures.

It is also a common experience to find mitochondria gathered in the peripheral cytoplasm, especially in egg cells. In cell division mitochondria are distributed approximately equally to the daughter cells. They are often radially disposed about the centrosome. Numerous other

6 Bensley, R. R., *Am. J. Anat.*, *19*, 37–54, 1916.

7 Lewis, M. R., and W. H., *Am. J. Anat.*, *17*, 339–401, 1915.

modifications have been noted, dependent upon variations in pressure and other obvious causes, but not a shred of evidence has been found that mitochondria possess powers of independent motility like some bacteria, which would explain the changes in position.

(4) *Amount.* In young embryos most of the cells contain approximately the same number of mitochondria per unit volume of cytoplasm. As development advances distinctive differences in the amount of mitochondria arise with the specialization of tissues. They are sometimes relatively more abundant soon after birth than in adults, notably in the pancreas and the thyroid. It has already been mentioned that they disappear as the cells become senile. To estimate these alterations quantitatively is particularly difficult in gland cells on account of the cyclical changes in volume, but a beginning has been made in nerve cells by Thurlow[8] who worked out a method of counting them in unit areas. She found marked differences in the relative amount of mitochondria in the cells of certain cranial nerves, thus contributing a line of advance which should be extended to pathological conditions.

(5) *Chemical constitution.* The suggestion that mitochondria are phospholipins in protein combination has come from three chief sources: From Regaud's[9] study of mammalian tissues, from Fauré-Fremiet's[10] work on protozoa, and from the investigations of the botanist Löwschin[11] which have unfortunately not been confirmed. In character it is largely negative. They do not color with Sudan III nor exhibit any of the properties of polysaccharides. Neither do they apparently contain appreciable amounts of iron in protein combination (Macallum's test). Berg,[12] Noël[13] and others have applied Millon's

[8] Thurlow, M. DeG., Contrib. Embryol. (Carnegie Inst.), Washington, *6* (16), 35–44, 1917.

[9] Regaud, Cl., Compt. rend. Soc. de Biol., *65*, 718–720, 1908.

[10] Fauré-Fremiet, E., Arch. d'Anat. micr., *11*, 457–648, 1910.

[11] Löwschin, A. M., Ber. d. deutsch. bot. Gesellsch., *31*, 203–209, 1913; *32*, 266–270, 1914.

[12] Berg, W., Arch. f. mikr. Anat., *96*, 54–76, 1922.

[13] Noël, R., Arch. d'Anat. micr., *19*, 1–158, 1923.

reagent quite extensively to liver cells without obtaining a pronounced coloration of mitochondria. But mitochondria do occasionally blacken with osmic acid. They are soluble in alcohol, ether, chloroform and other similar reagents unless they have been rendered relatively insoluble by fixation. Preservatives containing acetic acid in a concentration of from 5 to 10 per cent. usually destroy them. In appropriately fixed tissues, they are strongly fuchsinophile and stain sharply with iron hematoxylin. Perhaps their most striking characteristic is their affinity in living cells for Janus green B, which will color them in a dilution as great as one in half a million of physiological salt solution. If, however, H_2 or $(CH_3)_2$ is substituted for the $(C_2H_5)_2$ group in the compound, the specificity is lost.[14]

When we speak of homology between the mitochondria of different cells, we can only do so tentatively and with due qualification because, upon the discovery of more exact methods, further differences in composition may be brought to light. In other words, we have before us material exhibiting certain general properties in all living and active cells but which nevertheless varies to some extent in its attributes just as chromatin does.

(6) *Nature*. So close is, in some cases, the morphological resemblance between mitochondria and bacteria that investigators have from time to time asserted that they are in truth living microorganisms. This was the opinion of Altmann[15] who deserves credit for the prominent part which he took in bringing them to our attention (1880–1890). But his colleagues in Leipzig and in other parts of Germany did not receive his suggestion with enthusiasm, partly because he conceived the ground substance to be a lifeless substratum. Several years later, Portier[16] strongly advocated a somewhat similar view

[14] Cowdry, E. V., Contrib. Embryol. (Carnegie Inst.), Washington, *8* (25), 39–160, 1918.

[15] Altmann, R., "Die Elementarorganismen und ihre Beziehungen zu den Zellen." Leipzig, Veit and Co., 145 pp., 1890.

[16] Portier, P., Compt. rend. Acad. d. sc., *165*, 267–269, 1917.
"Les Symbiotes," Paris, Masson and Cie, 315 pp., 1918.
Compt. rend. Soc. de Biol., *82*, 247–250, 1919.

that mitochondria are symbiotic bacteria but his contention has not been favorably received[17] and the same idea advanced independently in the United States by Wallin[18] has also been questioned.[19] The generalization proposed is indeed so far-reaching in its application that the need for clear-cut information has been emphasized in a recent editorial published in the *Journal* of the American Medical Association.[20] The salient point of the discussion seems to be the manner of interpretation of the differences which undoubtedly exist between mitochondria and bacteria. Wallin is of the opinion "that mitochondria are symbiotic bacteria in the cytoplasm of all higher organisms whose symbiotic existence had its inception at the dawn of phylogenetic evolution." It is natural that during millions of years their properties would become somewhat changed from free living bacteria and he is inclined to explain some of the differences on this basis. Whether all differences are of a kind which may reasonably be expected to arise in this way I seriously question. Neither can I accept his contention that other organisms which have enjoyed a symbiotic relationship for a relatively short time approach mitochondria in their properties to a degree which would lend any support to his theory. This he has claimed for the *Bacillus radicicola* and the parasite of Rocky Mountain spotted fever as described by Wolbach, but very recently these organisms have been clearly differentiated from the mitochondria lying side by side in the same cell.[21] Not

[17] Regaud, Cl., Compt. rend. Soc. de Biol., *82*, 244–247, 1919.
Laguesse, E., *Ibid.*, 337–339.
Guilliermond, A., *Ibid.*, 309–312.
Rasmussen, A. T., J. Comp. Neurol., *31*, 37–49, 1919.
Van Gehuchten, P., Compt. rend. Soc. de Biol., *84*, 652–654, 1921.
Caullery, M., "Le Parasitisme et la Symbiose," Doin, Paris, 1922.
Levi, G., Monit. Zool. Ital., *33*, 99–118, 1922.

[18] Wallin, I. E., *Am. J. Anat.*, *30*, 203–229, 451–467, 1922. *Anat. Record*, *25*, 154, 159, 1923. AM. NATURALIST, *57*, 225–261, 1923.

[19] Cowdry, E. V., and Olitsky, Peter K., *J. Exper. Med.*, *36*, 521–533, 1922.

[20] J. Amer. Med. Assoc., *79*, 1848, 1922.

[21] Cowdry, E. V., Am. J. Anat., *31*, 339–345, 1923.
Nicholson, F. M., J. Exper. Med., *37*, 221–230, 1923.

only is there a very great gap between the properties of bacteria which have developed the most perfect degree of symbiosis known to us and mitochondria, but the positive data which has accumulated regarding the latter does not readily lend itself to interpretation in terms of this hypothesis.

A wholly different idea has dominated most of the work on mitochondria, namely, that during development they are transformed into many products of cellular differentiation,[22] a conception which falls well in line with the view that they are in part the material basis of heredity. A list of 80 substances, in the formation of which they are said to be concerned, was published in 1918. Many others may now be added. They comprise materials of the most diverse character, including glandular secretions, pigments, leucocytic granules, plant plastids, fibrillar structures of different kinds, fat, protein, glycogen, starch, urea, etc. That many of them are laid down either within the mitochondria or in their immediate vicinity is an observation of far-reaching importance which can not reasonably be questioned—the evidence contributed by Guilliermond through the direct observation of living plant cells is particularly convincing—but the likelihood that an actual transformation of mitochondria takes place naturally depends upon the difference in the chemical constitution of the original substance and the supposed end products, so that some of the claims involve chemical and physical improbabilities. The word transformation is certainly too definite and exclusive.

It was perhaps to overcome this objection that Regaud[23] advanced his famous eclectosome theory according to which the mitochondria play the part of plastids (into which some of them are known to develop in plants), choosing and selecting substances from the surrounding cytoplasm, condensing them and transforming them in their interior into infinitely diverse products.

[22] Meves, F., Arch. f. mikr. Anat., *72*, 816–867, 1908; *ibid.*, *92* (2), 41–136, 1918.

[23] Regaud, Cl., Rev. de Med., *31*, 681–690, 1911.

He compared them to the side-chains of Ehrlich. His theory is essentially a modification of the lipoid membrane conception of Overton, with this difference, that the lipoid is thought to be scattered throughout the cytoplasm, in the form of mitochondria, instead of being restricted to a layer upon the surface of the cell.

However this may be, to take part in the formation of certain products of differentiation is certainly not the only function of mitochondria, because we have already remarked upon their universal occurrence in embryonic cells before the onset of specialized activities. Impressed by their wide distribution, investigators have felt obliged to entertain the view that they are also concerned in some very fundamental vital phenomenon. Many have suggested metabolism; a few others, respiration; further study alone can decide.

(7) *Changes in pathological conditions.* Since mitochondria differ radically from the nucleus, the hope has been frequently expressed that their study will open an entirely new chapter in cellular pathology.[24] This expectation seems likely to be fulfilled because they are purely cytoplasmic elements which it is reasonable to suppose will be much more directly concerned than the nucleus in the manifold adjustments which are constantly taking place between living cells and their environment. It is not surprising, therefore, that mitochondria have been somewhat hastily studied in a great variety of pathological conditions including acute and chronic infectious diseases, endocrine disturbances, tumors, different dietary states, injury of mechanical or chemical nature, etc., etc.

In the literature, a complication is added by the fact that mitochondria have come to the attention of investigators in many branches of the biological and medical sciences who have shown no hesitancy in the invention of new terms to indicate theoretical interpretations, morphological characteristics, physical consistency and a host of other observed and supposed properties, so that in practice we have to seek information under a variety

[24] See editorial J. Amer. Med. Assoc., 67, 813, 1916.

of headings of which the following are most important:[25] chondriokonten, chondriosomen, chondriorhäbden, chondrioplasten, chondriosphären, chromochondria, karyochondria, myochondria, plastosomen, plastochondrien, vermicules, perinème, mitogels, mitosols, and fuchsinophile and interstitial granules (in part).

At this stage it requires some knowledge and no little imagination to select any type of injury in which the mitochondrial changes have not already been touched upon, usually by the examination of human tissues taken at operation, or at autopsy in which adequate control is out of the question, for the reason that the conditions can never be exactly duplicated. Failure to recognize the fact that a delicate indicator of cellular injury, like a new chemical reagent, is likely to be misleading is responsible for some disappointment in the results obtained. However precise the instructions may be the technique can not properly be shifted on to the shoulders of a technician. The methods require some adjustment to each tissue and must be standardized by frequent repetition. Even a slight and apparently trivial deviation from routine will often produce unexpected and profound alterations in the mitochondria. Pinching the tissues with the forceps or letting their surfaces dry in air will render them useless for accurate work. Much has been written about the necessity of taking them from the body immediately after death. This depends, naturally, upon the rate of autolysis. It is essential with glands and less so with the nervous system.

For many years the study of mitochondria in pathology will demand the painstaking observation of their behavior in animals held under experimental conditions which are capable of rigid control. We have to work over in detail ground which has been hastily scanned by our predecessors. But in this slow and systematic review, a good beginning has already been made.

[25] Cowdry, E. V., Anat. Record, *22*, 239–250, 1921.
The term ''mitochondria'' (thread granules) is derived from the Greek *μίτος*, a thread, and *χόνδρος*, a grain.

It has been shown, for example, that mitochondria are very much more sensitive in some tissues than in others. In glands they often respond by a loss of filamentous shape a considerable time before the nuclei exhibit any noticeable modifications. This has been found in experimental phosphorus poisoning by Scott,[26] who made the further observation that they are concerned in the resultant fatty degeneration. Nicholson[27] has brought to light a variety of mitochondrial changes in the thyroid which, as in the case of phosphorus poisoning, would probably have been completely overlooked in ordinary preparations fixed in Zenker's fluid and stained with hematoxylin and eosin. Other instances of the extreme susceptibility of mitochondria in gland cells might be cited from the almost overwhelming literature.

It is quite otherwise with the nervous system in which mitochondria respond to serious injury like axone section,[28] but show no very characteristic changes in beriberi,[29] functional exhaustion,[30] hibernation,[31] poliomyelitis,[32] and experimental herpetic encephalitis.[33] No explanation has been vouchsafed to explain this variability in reactivity, but it may be a function of the properties of the cytoplasm in which the mitochondria are imbedded and may not signify any radical differences in the mitochondria themselves.

Three general modes of mitochondrial reaction are recognized—qualitative, quantitative and topographical—which may occur singly or in combination.

By far the most delicate qualitative response is a change of filamentous mitochondria into granules. It is so delicate that it is often produced through injury caused by faulty technique alone. We have already men-

26 Scott, W. J. M., *Am. J. Anat.*, *20*, 237–253, 1916.
27 Nicholson, F. M., *J. Exper. Med.*, 1924.
28 Luna, E., *Anat. Anz.*, *44*, 413–415, 1913.
29 Clark, E., *J. Comp. Neurol.*, *24*, 61–110, 1914.
30 Strongman, B. T., *Anat. Record*, *12*, 167–171, 1917.
31 Rasmussen, A. T., *J. Comp. Neurol.*, *31*, 37–49, 1919.
32 McCann, G. F., *J. Exper. Med.*, *27*, 31–36, 1918.
33 Cowdry, E. V., and Nicholson, F. M., *J. Exper. Med.*, *38*, 695–706, 1923.

tioned its occurrence in the pancreas in phosphorus poisoning, and in the thyroid under a variety of conditions. It is common in inanition[34] and has been repeatedly observed in the living cells of tissue cultures.[7] Evidently cytoplasmic conditions favorable to a filamentous type of mitochondria may be upset or disturbed in a variety of ways, so that the change to granules can not be regarded as in any sense specific. We can not tell whether the injury acts directly upon the mitochondria or whether the morphological changes are only the visible expression of a long line of interdependent chemical reactions. Occasionally an increase in the girth of mitochondrial filaments is to be noted, but very rarely are they observed to elongate as a result of injury. Quite frequently they swell up into droplets with pronounced fatty and lipoidal properties. These alterations in form will probably remain obscure until we are able to correlate them with chemical changes by the aid of more exact methods for the detection of the lipoidal and protein fractions which probably enter into the composition of mitochondria. Changes in the shape of mitochondria produced in living cells outside the body by the action of hypo- and hypertonic solutions, by acids and bases, and by alterations in temperature are interesting and significant, but the limited range of variation in these qualities of the circulating blood precludes their operation except in a minor degree and we are left to explain why mitochondria existing side by side in the same cell, and presumably sharing most influences of this kind in common, often differ so greatly in morphology.

Quantitative changes are equally likely to be misleading. Even with uniformly fixed tissues unless the stain is differentiated to exactly the same extent an illusory impression of decrease or increase in mitochondria may easily be created. With rare exceptions, the observations recorded in the literature are merely based upon the gen-

[34] Miller, S. P., *Anat. Record, 23,* 45, 205–210, 1922. Okuneff, N., Arch. f. mikr. Anat., *97,* 187–203, 1923. Ma. W. C., *Anat. Record, 25,* 157, 1923.

eral appearance of sections. But few investigators have availed themselves of Thurlow's[8] method of counting the mitochondria in unit areas[31] and have taken the trouble to measure the variation in the size of the cells.[13] A diminution in the number of mitochondria is often met with in pathological conditions, but an increase above normal is rare. It has, nevertheless, been reported in toxic adenomata of the thyroid,[35] in the islets of Langerhans of the pancreas during diabetes,[36] in the kidney following the administration of phloridzin,[37] in regeneration[38] and, under the heading of Altmann's granules, in compensatory hypertrophy.[39] In tumors great variability in the number of mitochondria has been noted.[40] It is, I think, safe to assume that a decrease is to be considered a sign of depression of functional activity and that an increase is indicative of heightened activity, provided that they retain their normal shape, but when the increase is manifested by a swelling up of mitochondria into rounded droplets of different sizes, the condition is apt to pass insensibly into a simple accumulation of fat and lipoid which would point, on the other hand, to a decrease in the rate of intracellular oxidation. For the present, even a conspicuous increase in filamentous and rod-like mitochondria or of tiny granules hardly justifies the conclusion that any specific type of physiological process is enhanced, but it does show that the cells are not in a dormant or inactive state.

35 Goetsch, E., Johns Hopkins Hosp. *Bull.*, *27*, 129–133, 1916.

36 Homans, J., *J. Med. Research*, *33*, 1–51, 1915.

37 Policard, A., Arch. d'Anat. micr., *12*, 177–288, 1910.

38 Romeis, B., Anat. Anz., *45*, 1–19, 1913.
Torraca, L., Arch. f. Zellforsch., *12*, 539–552, 1914. Anat. Anz., *45*, 459–474. Arch. ital. di anat. e di embriol., *15*, 283–330, 1916.

39 Enderlen, Deut. Zeitschr. f. Chir., *41*, 208, 1908.
Hirsch, C., Anat. Hefte, *41* (1), 131–172, 1910.
De Giacomo, H., Intern. Monatschr. f. Anat. u. Phys., *28*, 208–232, 1911.

40 Veratti, E., Boll. Soc. Med. Chir. di Pavia, *23*, 34–45, 1909.
Beckton, H., Arch. Middlesex Hosp., *15*, 182–191, 1909.
Bensley, R. R., Trans. Chicago Path. Soc., *8*, 78–83, 1910.
Favre, M., and Regaud, Cl., Compt. rend. Soc. de Biol., *74*, 608–611, 1913.
Porcelli-Titone, F., Beitr. z. path. Anat. u. z. allg. Path., *58*, 237–249, 1914.
Sokoloff, B., Compt. rend. Soc. de Biol., *87*, 1202–1204, 1922.

By contrast, changes in the position of mitochondria within the cell are much less likely to result from imperfect technique. They have been reported in several conditions. The peripheral margination, discovered by Grynfeltt and Lafont,[41] is particularly noteworthy. A grouping of mitochondria about the nucleus is often met with in tumor cells and is generally, but not always, associated with a change in form. Here also we are at a loss to suggest any rational explanation and shall have to await an experimental analysis upon a fairly comprehensive scale of conditions which are associated with migration back and forth.

But mitochondria may possibly be of value in cellular pathology not only as indicators but in other ways. Recognition of the fact that they occur in the vast majority of living cells opens up a new line of study in the reexamination of the genesis of cytoplasmic inclusions of doubtful nature described before their discovery. For example, the large group of exanthematic diseases of unknown causation, including vaccinia, small pox, herpes, chicken pox and several others, that are less familiar, offer many remarkable cytoplasmic inclusions, concerning which more information is urgently needed.

(8) *Outlook for further study.* Unfortunately, the positive achievements of the study of mitochondria are as yet somewhat intangible. They constitute more than anything else a good augury for the future. However, when finally we attempt to take stock of the situation, several points become clear to us.

In the first place, it is quite obvious that the investigation of mitochondria will never achieve the usefulness which it deserves as an instrument for advance in biology and medicine until we know much more of their chemical constitution as the only accurate basis for interpretation of our findings. In other words, we must wait

[41] Grynfeltt, E., and Lafont, R., Montpel. med., *43*, 495, 502, 1921. Compt. rend. Soc. de Biol., *85*, 292–293, 406–408, 1921. Compt. rend. Acad. d. sci., *173*, 257–260, 1921.

upon the slow development of direct qualitative cellular chemistry.

Secondly, we have to admit that we are still, more than thirty years after the discovery of mitochondria, working very much in the dark. It is not greatly to our credit that these elements, which we can all clearly see at will in living cells, merely by the addition of a drop of janus green and the use of a good microscope, should continue to be such a profound mystery. Neither is it gratifying to find how relatively insignificant has been our progress in the last five or six years. We have a plethora of observations, but no new experimental method has brought us noticeably nearer to a solution of the puzzle.

We naturally search for new avenues of approach, and it is difficult to suggest any, but it is possible that we may use to better advantage methods already at hand. Even in experimental animals the physiologic processes are of such complexity as to be very baffling. To simplify matters we may have to resort to the systematic examination of pure lines of cells in tissue cultures by methods like those recently elaborated in a series of contributions by Carrel and Ebeling[42] which make possible quantitative study and the accurate analysis of cellular behavior in media of known chemical constitution. We may also profit by the very considerable advances made by W. H. Lewis and M. R. Lewis,[7] Levi,[43] and other cytologists with saline solutions as media. But further improvements are required even in a technique which achieves results that a generation ago would have seemed almost miraculous. It is desirable for one thing to approach still more closely to conditions in the living organism. The basis for ideal experimentation involves a method whereby living cells may be kept in good condition without evincing changes of a degenerative nature over a fairly long period of time, and by which cells of the same type show an equally uniform mitochondrial picture as in the living animal. This can only be accomplished by a

[42] Carrel, Alexis, and Ebeling, A. H., *J. Exper. Med.*, *37*, 759–766, 1923.

[43] Levi, G., R. Accad. d. Lincei, *31*, 425–428, 1922, and many earlier papers.

kind of artificial circulation providing for continual replenishing of the culture medium. Under the best of conditions interpretation will be difficult. It will not be possible, for instance, to say that the mitochondria, or the cells containing them, behave in exactly the same way as they do in the organism *in toto*. Since the cells find themselves unrestrained by the regulative processes to which they are accustomed, we may look for somewhat exaggerated reactions which take place at rates different from the normal. But with this limitation, advance along these lines may be instrumental in elevating the study of the cell to a truly experimental science dealing with variables that can be accurately measured and controlled.

There is still another point that I would emphasize. It is possible that students of mitochondria have approached too close to the problem to see it in its proper proportions. The tendency has been to single out the mitochondria and to observe closely their behavior under many conditions. The analogy is not very close, but the concentration of all our faculties upon the mainspring of a watch would not tell us very much unless its behavior were considered in relation to all the other parts of the mechanism. It is a sign of the times that more and more emphasis is being placed upon the interdependence of vital processes. Thus, Osterhout[44] is of the opinion "that life depends upon a series of reactions which normally proceed at rates which bear a definite relation to each other"—and "that a disturbance of these rate-relations may have a profound effect upon the organism, and may produce such diversive phenomena as stimulation, development, injury and death." Certainly, the most wonderful attribute of a living cell is the harmony of the chemical processes taking place within it. May we not profitably shift our method of approach and strive to modify cellular activity as nearly as possible in one direction only, and if possible to a degree that can be quan-

[44] Osterhout, W. J. V., The Harvey Lectures, New York, Lippincott, 1921–22, pp. 174–178.

titatively measured and then proceed to an intensive examination of the inter-relationships of the resultant structural and chemical changes? Correlations might well be effected between the composition of the medium in which the cells are living, some physiological attribute which can be measured and reduced to mathematical terms like growth, the size and internal morphology of the cells and their microchemistry. What might also be very helpful would be the direct observation of the physical condition of the cells by the methods of Kite and Chambers, who are responsible for the perfection of an apparatus for microdissection based upon Barber's pipette holder. The more skilful the analysis in selecting likely variables, and the more efficient the necessary organization, the better would be our chance to unearth phenomena causally related and thus to obtain an inkling of the method of integration of vital processes within the cell and of the part played therein by mitochondria.

Since the days of Schleiden and Schwann, cytology has been almost wholly an individualistic study. There have been no instances of the development of organization and cooperation at all comparable to that considered necessary in medicine and other applied sciences. As a rule, the cytologist attacks the most difficult and tricky of all problems—the nature of vital processes within the cell—armed only with a good microscope, a few chemicals, and an abundance of enthusiasm. That a more comprehensive and systematic approach will bear fruit is shown clearly by the work of Morgan and his associates in their experimental studies on the chromosomes.

Without dogmatism it may be said that our point of view in respect to mitochondria falls directly in line with the attention which is now being directed to physical forces acting at surfaces of separation between fluids of different character and density. Certainly one of the most fundamental features of cellular architecture is the presence of almost innumerable mitochondria which in the aggregate afford a surface far greater in extent than

that of the nuclear or plasma membranes. While fibrils, secretion granules, centrosomes and all other known products of protoplasmic differentiation are but short-lived and even the nuclear membrane is (during cell division) periodically lost and reconstituted, the mitochondria-cytoplasmic complex, alone, is inseparable from phenomena which we call vital and has so endured for years without number. The topographic association in the cell between mitochondria and chemical changes of great variety I have already mentioned. This is, happily, not a theory but a fact established by direct and repeated observation.

In concluding, it is not my intention in any sense to leave the impression that we are upon the threshold of the solution of this problem or upon the brink of any important discovery regarding the cell. However we proceed, many years of patient endeavor are required during which each of us will continue to use the methods which he is best qualified to handle. Inasmuch as we only dimly appreciate the meaning in cellular physiology and pathology of the more familiar surfaces of separation, we must steel ourselves to many disappointments before, with good fortune, we even approximate to a correct interpretation of mitochondria.

THE PROBLEM OF PATTERN IN ORGANISMS[1]

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I. GENERAL SURVEY

LIVING organisms are more or less distinctly defined and delimited individuals. An individual organism is an entity which possesses an order or unity of some sort which distinguishes it from its surroundings. Each organism possesses in some degree both morphological and physiological order and unity, and the problem of pattern is the problem of the basis and nature of this order and unity. Pattern, as the term is used here, includes not only the gross morphological and developmental pattern, but also physiological and physico-chemical pattern, that is, the pattern of the chemical reactions, the energy-transformations and transfers, the colloids and their changes, and so on. In fact, the problem of pattern in organisms in its broadest sense is the question, What is the organism? While we are still far from a complete answer to this question, it appears in the shifting light of biological research now in one aspect, now in another, and every advance in knowledge makes necessary a new consideration of it. The following discussion is concerned primarily with certain physiological aspects of the problem and with the bearing upon it of certain lines of recent investigation. The conception of the unity and order, that is, the pattern, of the organism, which is presented in this paper has developed from an extensive

[1] This paper, essentially in its present form, was written and accepted as a contribution to the proposed Williston Memorial Volume. Publication of that volume having proved impossible, the paper is dedicated to the memory of Professor Samuel Wendell Williston, both as an expression of personal regard and as a record of the purpose for which it was originally intended. The paper represents in considerable part the combined subject-matter of several addresses given at the University of Washington, the University of Wisconsin, the University of Cincinnati and elsewhere.

foundation of experiment and observation, but in the interests of brevity and in order to clear the ground, it is desirable to consider the problem in certain of its more general aspects before taking up the data on which the conception is based.

Protoplasms and Organisms

The problem of pattern always involves a problem of material or substratum. The order and unity which we call pattern always appears in some sort of material of substratum. The house represents a pattern superimposed upon the material, brick, stone, iron, wood, etc., of which the house is built. The organism likewise represents a pattern of some sort, arising in some way, in the material or substratum which we call protoplasm. Each of the materials of which the house is built also involves a problem of material and pattern different from that of the house as a whole. The brick, the stone, the iron, the wood, each represents a certain sort of unity and order in a certain sort of substratum, and the analysis may be continued down to the molecule, and if we define the term "material" very broadly, even to the atom. In the case of protoplasm also a similar analysis is possible. In other words, integrations or individuations of different orders of magnitude exist. The molecule represents an integration of a higher order of magnitude than the atom, the brick, stone, iron, wood, on the one hand, the colloid particle and all the other constituents of the complex system, protoplasm, on the other, involve one or more integrations of a higher order of magnitude than the molecule. The house and the organism again represent still further integrations, and houses may be integrated into town patterns, organisms into social groups of various orders of magnitude.

From this viewpoint the organism represents an integration, a pattern of a certain order or certain orders of magnitude, occurring in protoplasm as a substratum. Moreover, since it is concerned with masses of proto-

plasm, with cells or with cell masses, it is evidently of a higher order of magnitude, *i.e.,* on a larger scale, than the pattern of protoplasm. Similarly, the pattern of a multicellular organism is of a higher order of magnitude than that of the cell. The organism is then first of all an integration of protoplasm into a unity of some sort and, in its more complex forms, an integration of simpler organisms, the cells, or of tissues and organs, each consisting of numbers of cells. In view of this distinction between protoplasm and organism the word "organismic" becomes as necessary as the word "protoplasmic." All that pertains to the higher order of magnitude of pattern and integration in the organism, as compared with the protoplasm of which it is composed, is organismic, as distinguished from protoplasmic. I have used the word in this sense in earlier publications, but it was used much earlier by Rhumbler, and Ritter has recently used the word "organismal" in a somewhat similar sense.

Certain Characteristics of Organismic Pattern

In the preceding section the organism has been designated as an integration. If this integration is physiological, *i.e.,* physico-chemical in character, rather than a manifestation of a metaphysical principle, as the vitalists assume, it must involve relations of dominance and subordination, of control and being controlled. As a matter of fact, relations of this sort are apparently among the most general physiological characteristics of organismic pattern. Such control is exerted, on the one hand, by the transmission of energy-changes, on the other, by the mass transportation of chemical substances from one part to another. The transmissive type of dominance attains its highest development in transmission of excitation in the nervous system, together with its receptors and effectors, and the transportative type of dominance, in the complex "chemical correlation" of the higher animals, particularly in the products of the endocrine glands. In addition to these physiological features of organismic pat-

tern, a visible spatial pattern exists or arises during development. This consists in a more or less definite order of localization and differentiation, both as regards spatial arrangement and sequence in time, of different parts, the tissues and organs. We know that the existence and development of these parts is physiologically determined, and there is every reason to believe that the morphological pattern of the organism must be in some way dependent upon its physiological pattern. In short, such pattern must represent the more stable and permanent effects or results of physiological processes.

Moreover, the capacity of the organism for regaining or approaching its original condition after disturbance of that condition appears in the morphological, as well as in the physiological features of pattern. This capacity for regulation, whether it be regulation of behavior or development of a new complete individual from an isolated part, indicates clearly enough that the organism is not simply a preestablished harmony in a mosaic of independent parts, but a real unity in which dominance and subordination are real and effective to a high degree. Even normal development, with its highly definite and constant sequence and spatial order of events, shows every indication of being, at least primarily, a controlled and ordered process. Specialization of parts may sooner or later limit their capacity for response to altered conditions by change in behavior, but such limitation does not constitute evidence against the existence of a relation of dominance and subordination in development. The facts indicate that the limitation of regulatory capacity is itself a result of this relation. When, through its relations with other parts, a part has been determined in a certain direction of specialization, it is often able to progress along the predetermined path, even after isolation from the factors which originally determined it.

Again, the relation which we commonly call coordination is in reality a complex of relations of dominance and subordination. In short, all the evidence indicates that a

fundamental characteristic of organismic pattern is a system of physiological relations of control and being controlled. These relations show all degrees of fixity. Some change from moment to moment, *e.g.*, the relations between various reflex arcs in the higher animals and man, while at the other extreme we find relations such as those associated with physiological polarity and symmetry, which either persist throughout the life of the individual as actual relations of dominance and subordination or determine directly or indirectly structural or functional conditions which are persistent. The question of the nature and origin of these physiological relations is at least an important part of the problem of organismic pattern.

Theories of Organismic Pattern

Some biologists have maintained that a problem of organismic pattern does not exist, that the organism is nothing but a mosaic of cells or protoplasmic parts. According to this view, the only problem of pattern is that of the cell or of protoplasm. This is very much as if we should say that the pattern of the house is really given in the patterns of the single bricks or stones and that, given the proper number of bricks or stones of the proper patterns, they must of necessity arrange themselves to constitute a house. We know that bricks and stones do not behave in this way, but certain biologists hold that the living cells have the inherent ability to make a multicellular organism.

So long as our knowledge of living things was based on superficial observation and introspection there was little doubt that the organism represented the working of an agency fundamentally different from anything in the inorganic world. This "vitalistic" conception has undergone modification with the advance of experimental method in biology. In its modern form it holds that the integration, the harmony, the capacity for regulation or adjustment, can be accounted for only in terms of a meta-

physical entity or principle which works in a purposive manner, that is, as if intelligent. The "neovitalistic" conceptions have the merit of recognizing that the problem of organismic pattern exists and is of fundamental importance, but all the solutions of the problem which they have offered thus far involve assumptions or generalizations which are not only premature, but which involve the more or less complete negation of scientific method.

The so-called preformistic conceptions of the organism, ranging from Bonnet's theory of "emboitement" to the Weismannian germ plasm with its determinants, ids and idants and the still more recent modifications of the conception, either assume the existence of organismic pattern in the hereditary constitution of the germ plasm, or ignore the problem. Weismann's integration of determinants into patterns of various orders of magnitude and the apparent belief of certain more recent preformists that the pattern of the organism is given in the intranuclear or chromosomal pattern all involve the assumption of the existence of organismic pattern, but throw no light on the problem of its nature and origin. The more recent preformistic conceptions are chiefly concerned with the supposed elements of the pattern rather than with the integration of these elements into a harmonious whole. It is evident, however, that if we conceive the elements of organismic pattern as discrete and persistent hereditary entities, whether we call them determinants, factors, or something else, we must also conceive some sort of controlling or ordering factor to account for the harmony and constancy of result in their developmental and regulatory behavior. But the preformistic theories have failed to provide any adequate physico-chemical basis for such an integrating factor. From this viewpoint they are to a greater or less degree vitalistic in implication, that is to say, they not only fail to give us an adequate physico-chemical basis for integration, but it appears that nothing short of a metaphysical principle,

working intelligently with all physico-chemical agencies under its control, can be conceived as adequate for the ordering and integrating into a harmonious whole the inconceivable multitude of postulated hereditary entities.

Various attempts have been made to formulate more or less strictly preformistic conceptions of the organism in terms of molecular, or intermolecular relations. Such, for example, are the suggestions that factors similar or analogous to those concerned in determining the integration and form of the crystal are the primary factors in organismic pattern and various other suggestions based on stereochemical conceptions. We even find the view advanced that the germ plasm is to be conceived as a single complex molecule. In view of the physico-chemical complexity of protoplasm, the absence of any optical or other indications of a static molecular or stereochemical arrangement in protoplasm in general, and the rôle of chemical reaction in growth, development and function, these hypotheses have not generally been found satisfactory as a basis for interpretation. Nevertheless, if a physico-chemical formulation of preformistic theories is possible, it must apparently be made in some such terms as these. If, for example, the chromosome is a physico-chemical entity and consists of a definite series of hereditary factors or genes, we can conceive it only in terms of stereochemical, crystalline or other physical order. But such a conception does not carry us far toward the interpretation of pattern in the cell or the multicellular organism: for this some sort of order on a larger scale is necessary.

The epigenetic viewpoint contrasts sharply with the preformistic in maintaining that relation between protoplasm and environment is a fundamental factor in determining organismic pattern and integration. Thus far, however, the epigenetic school has not advanced any very definite conceptions as to the nature of organismic pattern or the manner in which it arises out of the relations between protoplasm and environment. Moreover, the

high degree of constancy of course and results of development, as regards both form and function, has presented difficulties to epigenetic interpretation.

The problem of organismic pattern remains then a real problem and one which is forcing itself more and more on the attention of biologists. The following sections of this paper are devoted to a consideration of this problem in its physiological aspects, as viewed in the light of recent investigation. This consideration leads to an essentially epigenetic conception.

The Problem from a Physiological Viewpoint

Attention has already been called to the fact that the organism represents a pattern on a larger scale than that of protoplasm. It is an integration among regions or masses of protoplasm, or in multicellular organisms, among masses of cells. The cell itself is primarily an organism and the problem of its pattern is a part of the general problem. An organism consists, not simply of protoplasm or cells, but of protoplasms, cells or cell masses which behave in different ways and become different structurally, but constitute in each particular case a unity or harmonious whole, and it is this unity which constitutes the essential characteristic of the organism. If the organism is a physico-chemical entity, the integration of the protoplasm, cells or cell masses must be accomplished in some way by physico-chemical factors, but by such factors working on a larger scale than those concerned in protoplasmic constitution. In the organism physiological relations involve large areas of protoplasm or large numbers of cells and, either by means of transmission of energy changes or of mass transportation of substances, regions and parts separated by considerable distances are brought into relation. According to both vitalistic and preformistic conceptions, the organism arises independently of environment and enters into relation with it only after a certain stage is attained. As a matter of fact, however, the organism has no significance

apart from environment. Its pattern is the basis of its behavior in the broadest sense in relation to environment, and it stands in relation to environment at every point and at all times. The factors in this relation are accessible to scientific investigation, and we must first of all determine their significance for the origin and nature of organismic pattern. Only when it is finally proven that organismic pattern does not arise in relation to environment are we scientifically justified in falling back on speculative conceptions. For the present, then, the problem is a physiological problem.

In the past the distinction has not always been clearly drawn between the integrating factors in the organism and that which is integrated. Each kind of organism is made up of protoplasm with a specific constitution which we may regard as, at least in large measure, hereditary, and therefore as given for any particular individual. It is this specific constitution of the protoplasm which determines that the organism shall be a certain species, whether alga, sea urchin, dragon fly, fish, etc. On the other hand, the organismic pattern in the strict sense is not concerned in determining the particular species of organism, but merely in integrating and ordering the process of realization of the hereditary potentialities of the protoplasm so that the unity which we call an organism results. In other words, organismic pattern does not belong primarily among the hereditary potentialities of any particular protoplasm, but is a physiological factor concerned in the orderly realization of those potentialities or certain of them, in the development and function of all protoplasms.

If organismic patterns were inherent in, or associated with the specific hereditary constitution of the various protoplasms, we might expect to find a specific organismic pattern for each specific protoplasm. As regards various minor details we do of course find such specific differences in pattern, but as regards the more general features it is far from being the case. The pattern of the

cell or protoplast, for example, is fundamentally similar in animals and plants. In multicellular organisms also we find very similar patterns composed of very different protoplasms. In their more general features the patterns of hydroid colonies and of certain multiaxial plants resemble each other very closely, not only as regards form of the whole and arrangement of constituent members, but as regards the physiological factors which determine the relations of growth and form in the whole. Differences in physiological condition along the axis are very similar in both, and a physiological relation of dominance and subordination integrates the whole in essentially the same way in both. Again, the bilateral liverworts, *e.g.*, *Marchantia,* and the bilateral flatworms, such as *Planaria,* are very similar as regards the general axiate-symmetrical pattern, and in the one case the growing tip, in the other the head region, is dominant over a certain length of body.

In fact, there is apparently no relation between the more general and fundamental features of organismic pattern and the differences in specific hereditary constitution of the different protoplasms. There are in all organisms only three chief types of spatial order or pattern, as indicated by the general arrangement of organs and parts. The pattern may be radially symmetrical, referable to a point, polar, referable to a line, or bilateral, referable to a plane. Localization and differentiation of parts in all organisms, so far as we know, occurs according to one of these three orders, or some combination or modification of them. The cell is perhaps primarily a completely radiate or spherically symmetrical organism, a surface-interior pattern. Both plants and animals show various combinations of radial, polar and bilateral pattern, and asymmetries or spiral patterns appear in some organisms. Physiologically the relation of dominance and subordination is apparently the fundamental relation in organismic integration in both plants and animals. In short, the three sorts of spatial pattern

and the relation of dominance and subordination appear to be the primary features of organismic pattern, and the question is whether we can discover any physiological basis for them.

Between the parts of an organism physiological correlation exists. Leaving out of account the purely mechanical relations of pressure and tension, which are obviously not of fundamental importance, two chief groups of correlative factors are distinguishable. These are, chemical or transportative, involving the mass transportation of substances over appreciable distances, and excitation-transmission, involving first the excitation of some region and second the transmission of the excitation through a greater or less distance.

If organismic pattern is not inherent in protoplasm, it is evident that chemical or transportative correlation can not be the primary physiological factor in such pattern, because definite and orderly transportative correlation on an organismic scale is possible only when organismic pattern is already present and differentiation of different regions or cells has occurred. After such differentiation has occurred, transportative correlation becomes possible and increases in complexity and importance with the progress of differentiation, but it can not originate the pattern on which its existence depends.

Turning to transmissive correlation, several points may be noted: First, that all living protoplasm is excitable and to some degree capable of transmission; second, that excitation is not autonomous, but results in the final analysis from action of an external factor; third, that excitation and transmission may occur in a cell or cell mass without any previous specialization or differentiation of either the region of excitation or the path of transmission; fourth, that in the absence of definite conducting paths excitation undergoes a decrement in degree, intensity or energy in the course of transmission and is therefore limited in range; fifth, that the region of original excitation becomes for the time being physiologically domi-

nant over other regions within the range of transmission, because it is the initiating factor in the correlation.

In its primitive form, then, this excitation-transmission relation represents a gradient in physiological state, or degree of excitation, arising in protoplasm in response to the local action of an external factor. As long as it persists, it constitutes a pattern, a physiological integration different from any inherent feature of protoplasmic pattern. In fact, the excitation-transmission relation appears to be the most general and most primitive relation *of organismic magnitude* possible in protoplasm. If organismic pattern originates in the relation between protoplasm and an external world, it appears from what has been said that the excitation-transmission relation must be the most general and most primitive factor in such pattern.

THE SPECIFICITY OF FOOD-PLANTS IN THE EVOLUTION OF PHYTOPHAGOUS INSECTS[1]

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THE great variety of foodstuffs acceptable to the insect palate is well known and accounts in part for the great abundance and variety of this group of animals. Coupled with their catholic tastes as a group is the anomalous condition that the vegetarian members of the series not only show far less latitude in selecting their food than do other herbivorous animals, but are as definitely restricted in their choice of food as are parasitic animals. These facts are so self-evident and have been so frequently commented upon that their evolutionary significance has been very generally overlooked. In fact, the present interdependence of insects and plants is so complex that the simpler relations of individual species to particular food plants seem by comparison to offer little to interest the present student of biology. If we inquire more closely into the matter, however, it is seen that they offer not only an interesting field for speculation, but opportunities for the application of experimental methods.

Quite naturally almost all our knowledge of the specificity of food-plants and their selection by phytophagous insects is based on direct observations of the behavior of a great many species in nature. Deductions drawn therefrom emphasize particularly the great nicety of adaptation exhibited by the insects, their fixed and almost immutable behavior, the delicacy of their senses in recognizing certain plants, and, finally, the coordination between the egg-laying instincts of the mother and the food-appetites of her larval offspring, however greatly their food may differ from her own.

[1] Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 233.

I have already attempted to point out in The American Naturalist (Brues '20) and elsewhere ('23) what vast differences exist between polyphagous, oligophagous and monophagous insects so far as the extent of their diet is concerned and some of the conclusions that may be drawn therefrom. On this basis, such groups appear to be more or less fundamentally distinct one from another, although attention has been drawn also to the fact that among polyphagous and oligophagous species there are certain preferred food-plants. This at once suggests a greater plasticity in the organization of these insects which we may regard as due either to more variable instincts, less restricted powers of digestion and assimilation, or to the occurrence within species of races possessed of predilections for only certain of the food-plants that make up the diet of the species as a whole. Such a combination of physiological races is essentially analogous to the concept of impure species as composites of pure lines, except that it involves behavioristic and not morphological characters. Although there is much evidence to support the validity of such a comparison, the matter has not been subjected to the careful experimental scrutiny bestowed upon the morphological composition of species. Nevertheless, as we shall see in a moment, it appears very probable that in at least some polyphagous insects there are phytophagic races whose food-habits are clearly different and that each type is maintained through heredity under natural conditions. It is thus probable that crossing between such races does not normally occur, at least to any appreciable extent, although in polyphagous species having a wide range of food-plants there appears so far to be no evidence to indicate selective mating between individuals either from the same or from different food-plants. The small amount of evidence actually relating to known hybrids, which will be presented later, is very fragmentary and of contradictory nature.

The fact that some species of insects include groups of individuals having different food-preferences seems first

to have been recognized by the pioneer American entomologist, Benjamin Walsh, who wrote quite extensively ('64 and '65) on the subject and drew conclusions based not only on close observation of insects in the field, but also on some experiments which he performed with several species in confinement. Walsh was satisfied that there existed intraspecific groups of individuals with different food preferences, showing sometimes no structural differences, sometimes slight structural differences in the larva, and sometimes also in the imago. Such groups he believed were incipient species, having acquired a hereditary preference for certain food-plants and destined to diverge more widely in the course of time. Written so soon after the appearance of Darwin's "Evolution of Species," Walsh's account is in part combative of the doctrine of special creation, and his cases are cited with reference to evolution as influenced by isolation arising from the attachment to particular food-plants. He does not, therefore, speculate to any extent on the shifts to new food-plants, nor on the way in which such changes may have become fixed. Some of Walsh's work is cited more specifically on a later page.

After the lapse of a number of years, Cockerell ('92) presented a short note in which he attempted to explain the segregation of phytophagic types among polyphagous insects and also the shifts to new food-plants, on the basis of the principles of natural selection. A part of his thesis rests upon the occurrence of intraspecific variations that tend to feed and develop more satisfactorily on certain particular ones of the food-plants normally eaten by the species as a whole. His ideas are closely similar to those of Walsh.

During the present century a number of entomologists have given their attention to the facts just referred to, and the behavior of certain insects in relation to their food-plants has been further studied, although Walsh's papers seem to have been overlooked.[2]

The small Trypetid fly, *Rhagoletis pomonella,* fur-

[2] A discussion of Walsh's work by Craighead ('23) has since appeared.

nishes an unusually clear case of a single species which is represented by two distinct forms or races that are restricted to different food-plants, although they show absolutely no morphological differences except for a quite constant difference in size. This insect appears to be undoubtedly native to North America, and it seems very probable that it originally bred in the fruits of certain species of Crataegus. On account of its great economic importance, it has been carefully studied by several entomologists, Comstock ('82), Harvey ('90), Illingworth ('12) and O'Kane ('14).

The apple-maggot has practically deserted its original food-plant and is now a very abundant and destructive pest of apples in New England, New York and Pennsylvania, extending also into the Middle West in much decreased numbers. The larvae mine within the fruits, especially those of the summer and early fall varieties. Several times during the past twenty-five years this insect has been reported as breeding in blueberries, and Woods ('15) has given a very entertaining and instructive account of a smaller race which is a common blueberry insect in some parts of the state of Maine. Woods finds noticeable differences in size in both the adults and larvae from the two plants; thus, the male flies from apple average 4.60 mm, those from blueberry 3.60 mm, while the females average, respectively, 5.80 and 4.20 mm in length. Similarly, the larvae are distinguishable on the basis of size, and although there is much variation in each series, in no case is there any overlapping between the two races. Furthermore, he finds that the smaller blueberry flies are much more active and more wary in their behavior than those from apple. Attempts to transfer the apple race to blueberry or *vice versa* were unsuccessful, even in the case of half-grown blueberry-maggots transferred directly into apples, and Woods concludes that he "is inclined very strongly to believe that biologically at least there are two distinct strains or races of *Rhagoletis pomonella* Walsh, the one breeding in apple and related fruits, and the other in smaller

fruits such as the blueberry and huckleberry. There does not seem . . . to be any other conclusion which will explain the data given above. Certainly, in so far as Rhagoletis occurs in Maine, the form on the apple and the form on the blueberry are entirely independent. The oldest inhabitant of the barrens can not remember a time when there were not maggots in the blueberries, while the introduction and spread of the apple maggot in the state is a matter of record. . . . In Maine the blueberry maggot apparently did not migrate to the apple nor *vice versa* and the two races have lived on independently side by side."

The leaf-beetle, *Calligrapha scalaris,* feeds on a number of plants, and Walsh ('64) noticed that there are two types distinguishable by their size. The larger one, measuring 7–8 mm in length, occurs on elm and basswood, and the smaller, 5.5 to 6 mm long, he found on dogwood and wild plum.[3]

The quite sudden adoption of a new food-plant by the common butterfly, *Papilio zolicaon,* in California appears to be well authenticated (Coolidge '10). Like *P. asterias* of the eastern United States, *P. zolicaon* feeds upon various Umbelliferae, especially celery, parsley and Carum, but has been found abundantly in at least two localities in California on citrus fruit trees. Although this is a new habit for this species, the change may be in the nature of a reversion, since another group of Papilios of wide distribution feed on citrus.

The well-known codling moth, *Cydia pomonella,* is an abundant species of holarctic distribution which develops in the larval condition in the fruit of the apple. There is a race or form of this species, however, which feeds in walnuts and has become a great pest in certain parts of California where walnuts are extensively grown. In Europe a walnut form is also known, and this apparently is the one now found in California, as it does not appear

[3] On account of the difficulty of distinguishing the species of this genus, Walsh's observations are not conclusive (*v.* Knab '09). *C. philadelphica* feeds on Cornus.

that the insect has migrated directly from apple to walnut, although there appear to be no morphological differences between the two races (Foster '10; Smith '18).

The common alder flea-beetle of the eastern United States, *Haltica bimarginata* Say, feeds almost exclusively on the leaves of the alder, *Alnus incana,* both as a larva and adult, although it sometimes occurs on willow, poplar and cottonwood. Woods ('17) found it in Maine regularly on alder, and at one single locality on the balsam poplar (*Populus balsamifera*). Larvae obtained from eggs deposited on alder fed readily upon alder, willow and aspen (*Populus tremuloides*) but absolutely refused to eat leaves of the balsam poplar, although individuals obtained from balsam poplar readily accepted this plant as well as alder, aspen and willow. It appears evident in the case of this beetle that alder is the preferred food-plant for the species, but that a strain exists, at least in one locality, which will accept the balsam poplar, although it has not developed a distaste for alder.

The abundant and well-known caterpillar of *Lasiocampa quercus,* which formerly fed almost only upon oak, is now commonly found on a variety of widely different trees, and similarly *Abraxas grossulariata,* formerly restricted to Ribes, now feeds regularly on the foliage of oak, Euonymus and other woody plants.

That the acquisition of apparently new food-plants may really be a reversion or return to one formerly selected during the phylogenetic history of the insect appears probable in some cases. Thus, in France the nun moth lives almost exclusively on oak, but feeds on pine in Germany. Pictet ('05) regards the latter habit as a reversion to an ancestral food-plant, and if such be true the acquired oak habit may be regarded as probably kept up by a racial memory, liable to be overcome at any time by a more deep-seated phylogenetic tendency. We will see later that such a supposition finds some support in experimental work on racial memory extending over only two or three generations.

Examples like the Rhagoletis, Papilio, Cydia and Haltica just cited, have in some cases been explained not as sudden changes or mutations in habit, but as having an evolutionary or historical significance. Thus, Vassiliev ('13) during a study of beet-insects in Russia found that a weevil, *Bothynoderus punctiventris,* regularly attacks two species of Chenopodium and one of Atriplex in addition to the beet (*Beta vulgaris*), all members of the Chenopodiaceae, but that it feeds also on *Polygonum aviculare.* Since the Chenopodiaceae and Polygonaceae are related, the author assumes that the weevil originated at a time when the relationship between these two groups of plants was closer, with more intermediate forms. This assumption necessitates a very rapid evolution of plants and corresponding inhibition of change in insects and does not receive any paleontological support.

Parallel evolution of insects and their food-plants where groups are concerned rather than isolated species is, however, much more plausible and the probability of this having taken place in many instances appears greater as we examine in detail the food habits of certain insects. In the case of the violet-eating Argynnid butterflies and similar groups, it appears very evident that evolution has proceeded concurrently among the plant and insect species. The Pierid butterflies are essentially feeders on Cruciferae, but a few genera affect Leguminosae. The family is widely distributed and has produced many forms restricted to crucifers, some living on Leguminosae, and a few, Catopsilia and Callidryas, restricted to the single genus Cassia in widely separated parts of the world. We can not be far amiss if we assume that the acquisition of a leguminous food-plant was a mutation or at least a sudden shift and that diversification of the insects has proceeded not necessarily with any reference to that of the plants, but that the two have gone on side by side, most of the insects gradually acquiring additional, although not necessarily very closely related, leguminous food-plants.

A most unexpected change in food habits was observed by Pictet ('11) in the course of experiments with the caterpillars of *Lasiocampa quercus.* Larvae of this species derived from oak, which, together with other deciduous trees, forms their normal diet, were placed on pine. Of these many died, as they could not open their jaws widely enough to remove the tissue from the pine needles. Some, however, survived by feeding at the ends of the needles where they can work into the parenchyma. The second generation was then found to be adapted to pine, on which the caterpillars fed without difficulty and furthermore they were unable to return to oak leaves, which they attempted to enter from the tip as their parents had done on the pine needles, although the larvae are normally edge feeders. Pictet's experiments certainly suggest that memory has played a part in the behavior of the second generation. Nevertheless, it is clear that there has been a selection of a few individuals in the first generation and that their offspring may be expected to inherit at least the power of adaptation to pine shown by their parents in adopting a new method of feeding. On the other hand, we should expect the offspring to be equally quick in readapting themselves to oak, which they do not appear to be. One other supposition may be made also, that there was a drastic selection in the parents which actually changed the form of the mouthparts sufficiently to make oak-feeding difficult. This latter does not seem very likely, but makes it necessary to regard Pictet's experiments as not entirely conclusive.

The food-preferences of a small leaf-mining fly, *Pegomyia hyoscyami,* have been studied in England by Cameron ('14 and '16), who finds that within this species there are groups which react differently toward the several food-plants upon which the larvae may develop. As the specific name indicates, the henbane (Hyoscyamus) serves as one food-plant, but another solanaceous plant, *Atropa belladonna,* is attacked as well as certain Chenopodiaceae, such as *Chenopodium album* and the cultivated beet and mangold.

It appears that ordinarily when henbane and belladonna are grown in proximity, the former is extensively damaged by the flies which avoid the belladonna, but that when henbane is absent the flies are attracted to belladonna, on which their larvae develop. Also, flies reared on belladonna will oviposit and develop on mangolds, if deprived of the parental food-plant; but, on the other hand, oviposition on beets by individuals reared on mangolds did not occur. These experiments could not be carried sufficiently far to demonstrate the behavior of the several broods toward different food-plants, but they show clearly the existence of a preference for the parental food and a varying ability or willingness to shift to others. In connection with this species it is worthy of note that the several forms of Pegomyia, some of which are well-known noxious insects, have extremely diverse habits, indicating a great plasticity of behavior and high degree of adaptability in the genus.

The change of an insect from one food-plant to another with a coincident change in structure has been reported by Marchal ('08) in the case of the soft scale, *Lecanium corni* (=*persicae*). The evidence, which appears to be well substantiated, is in brief as follows:

Marchal was led to believe from the presence of a Lecanium on the American tree, *Robinia pseudacacia*, naturalized in Europe that the insects had been derived from some native palaearctic species. The form on locust (*L. robiniarum*) is now scattered through various parts of France, but was unknown previous to 1881. Likewise, it was first found in America in 1892 by Cockerell in New Mexico far from the Appalachian ridge that represents the original habitat of *Robinia pseudacacia*. How extensive the insect may now be in America I do not know, but it was present near Boston in 1912.

By taking eggs from individuals of *L. corni* on a peach tree, and transferring them to locust, Marchal succeeded in establishing a brood upon locust and the adults on maturing showed "the large size, dark coloration and definitive habitus of *L. robiniarum*."

Attempts to restore these insects to peach were futile in the single experiment made by Marchal, and he concludes that the inverse change of food-plants is at least more difficult to make, although it may be possible.

Some experimental evidence relating to the memory of leaf-eating caterpillars, as indicated by their reactions toward undesirable food-plants, has been presented by Mayer and Soule ('06). They found that in the case of the common milkweed butterfly (*Anosia plexippus*), larvae that have commenced to feed upon a milkweed leaf may be induced to bite at leaves they would not normally eat if these be presented to the feeding larva at intervals of not less than a minute and a half. In such cases the larva takes the same number of bites each time after repeated trials, showing that it exhibits no distinct direct nor cumulative memory of such experiences. If, however, the unacceptable leaf be offered as frequently as each half minute, the number of bites taken decreases with each successive experience. This cumulative effect soon results in complete refusal to bite at a distasteful leaf.

Just how far such experiments bear on memory in relation to the selection of food is by no means clear. They show that the process of feeding in such caterpillars proceeds in a very mechanical way after it is once initiated and well in progress, that is to say in the case of the Anosia larva, after feeding for one and a half minutes, and that eating stops only after the different flavor is recognized by the insect. They show also that the larvae do not apply their previous experience in dealing with a specific problem when it is again presented after one and a half minutes, although the same caterpillars appear to do so if the occasion arise at the expiration of a half minute period. This is not in any sense the memory of a particular flavor or odor which must be the stimulus to be taken into account in any theory of associative memory applied to the selection of food-plants by adult insects that have fed in the larval stage upon particular

plants, and does not seem to shed any light on this question. That such is the case is also shown by the fact that the caterpillars in the experiments reacted in an identical way to strange leaves, paper and tinfoil, and thus regarded the world as composed of either "milkweed" or "not milkweed," just as the cabbage-worm arbitrarily divides its world into Cruciferae and other objects too numerous to mention.

A recent paper by Craighead ('21) contains a very interesting report on experiments upon longicorn beetles, undertaken to determine the possible modification of food-plant selection resulting from continued breeding in the wood of particular species of trees. For this purpose Craighead selected a series of beetles each known to have more than one food-plant in nature and examined the behavior during subsequent generations of strains of each species bred upon the several food-plants. Eleven species of beetles belonging to eight genera were used in these experiments, some confined almost exclusively to a single food-plant, some to two or three plants and some which attack a rather wide variety of trees.

Thus, *Cyllene pictus* feeds almost exclusively in hickory, although rare instances are known of its occurrence in grape, mulberry, osage-orange and hackberry. It was found that this species when obtained from hickory will readily adapt itself to grape and mulberry, and also to oak, although this does not appear to be a natural host. Furthermore, in the case of mulberry it was found that the hickory strain after breeding for one generation in mulberry selected the latter wood for oviposition in which the larvae then matured successfully. A similar transfer of this same strain to grape gave a somewhat more doubtful result. At this point, however, we must indicate some of the difficulties attendant upon these experiments. The selection may be influenced by the condition of the wood (as regards seasoning, moisture, etc.) and also by the amount of available material of each, since it appears evident that adults will prefer a secondary host to overinfesting the preferred one. Such dif-

ficulties are unavoidable, but can, of course, be minimized when they are thoroughly understood. Attempts to transfer this species to locust (*Robinia pseudacacia*) and ash (*Fraxinus*) were unsuccessful;[4] oviposition occurred, but all the resulting larvae in ash died as well as most of those in locust and as imagines resulting from the latter did not reproduce, they may have been sterile. A number of larvae from hickory, transferred to ash after they were half to three fourths matured, developed in the ash, but the resulting beetles appeared also to be sterile, as they failed to produce larvae when caged over both ash and hickory.

With the strain of this species obtained on grape, it was found that the first generation selected grape, but that the next generation attacked both kinds of wood.

Callidium antennatum, a species that occurs in seasoned pine, is known to occur in spruce also, but a strain from pine failed to reproduce in spruce when caged over both woods, although a single larva (which later died) was found in the spruce. Later in the season, Craighead transferred some half-grown larvae to spruce, in which they completed their development, and the emerging beetles in great part selected spruce the following spring and entirely so in the next generation the ensuing year.

Xylotrechus colonus is a widespread, polyphagous species that occurs in nearly all the hardwood trees of the eastern United States. A strain of this beetle obtained from oak showed a decided preference for oak, chestnut and hickory. It was barely able to maintain itself in ash and maple, but totally unable to complete its development in locust. By isolating from the original oak strain, separate series on oak, chestnut and hickory, after several years strains were obtained which exhibited a growing preference for the particular wood to which they had been restricted.

[4] Walsh ('64) regarded the locust form (*C. robiniae*) and the hickory one (*C. caryae*) as phytophagic varieties, but they are now generally considered as distinct species in which the specific differences are most clearly marked in the male.

The data obtained from the other species agree well with those cited above, although some were not so clear-cut. Although these experiments are not so complete and convincing as might be desired, they at least strongly support the validity of several conclusions. There can be no reasonable doubt that there is a general tendency for the individual beetles to oviposit more abundantly in the species of wood in which they themselves fed as larvae than in another which is from the standpoint of the entire population of the species more desirable. Furthermore, there appears to be an increasing degree of preference after additional generations, although in one case, that of Callidium, the adults of the third generation suffered a relapse, and, for some reason not evident, reverted to their original diet of pine. Considering the nature of the case, however, and the fixity of food-habits in general, reversions of this sort must be expected and if they do not invariably occur they do not disprove the conclusion expressed above. A second fact brought out by these experiments is that oviposition frequently occurs on woods that are not suitable food for the larvae, which consequently suffer a high or even complete mortality at an early age. This is in accordance with observations made on certain parasitic insects, cited in a previous paper (Brues, '21), where certain unsuitable hosts may serve for oviposition, but not for the successful development of the parasitic larvae.

Another instance which may possibly be interpreted as supporting Craighead's contentions has been reported by Hegner ('10). This relates to a Chrysomelid beetle, *Calligrapha bigsbyana,* the larvae of which feed normally on leaves of *Salix longifolia.* However, when Hegner reared larvae of one generation of *Salix amygdaloides,* their offspring were found to show no preference for their natural food-plant, but attacked both species of willow without preference.

An experimentally obtained shift of food-plants, involving not only considerable mechanical difficulty, but

finally resulting in a different method of feeding, has been reported by Schroeder ('03) in the leaf-beetle *Phratora vitellinae,* the larvae of which feed on the leaves of the willow, *Salix fragilis.* The leaves of this willow are smooth beneath and are skeletonized by the larvae which feed upon the underside, leaving intact only the superior epidermis. Larvae transferred to *Salix viminalis,* which has the leaves densely downy beneath, found feeding difficult, but the insects were able to push this material aside and reach the parenchyma of the leaf, and one actually avoided the pubescence and excavated a mine in the leaf-tissue. After four generations on the downy willow the larvae had gradually adopted the leaf-mining habit, and showed a greater percentage of choice for *S. viminalis* as the proportion of adults that selected this plant for oviposition increased from 9 per cent. to 42 per cent.

The results obtained by Schroeder appear to be strictly comparable to what might easily occur in nature as the result of the continued scarcity of a preferred food-plant.

Several observers have called attention to an ontogenetic cycle of changes which frequently occurs among the most diverse insects whereby there is a shift from one food to another during larval development. Cases where there is an extreme shift in food-habits associated with profound morphological changes do not concern us here, as they have a clearly structural basis. Those where the shift is less and involves merely the migration to a different part of the food-plant have a more direct bearing on the present discussion and I shall return to them in a moment. Quite similar to these is the phenomenon of alternation of generations exhibited so clearly in many hymenopterous gall-insects of the family Cynipidae. This involves also great structural differences in the insects and so many other as yet undetermined factors that its bearing on ancestral memory and related questions remains very obscure.

In some other groups of phytophagous insects, however, we find what appears to be an incipient alternation

of generations in very simple form, associated with a definite alternation of food-plants. For example, the European geometrid moth, *Tephroclystis virgaureata,* passes through two generations during the course of the season, the first brood of caterpillars feeding in the early spring on Compositae (Senecio and Solidago), and the second brood in midsummer feeding on Prunus and Crataegus (Klos '01). Furthermore, the adults of the two generations show small but constant differences in color. Many other similar cases are known, and undoubtedly the phenomenon is quite widespread among multivoltine insects, including some in which the food-plant is the same during successive generations. Such a condition prevails among numerous butterflies which exhibit a seasonal dimorphism related to, and perhaps entirely dependent upon temperature. Other cases of polymorphism, on the other hand, are known to be due to the different genetic constitution of the several types. The polymorphic females of one Papilio which have been described by de Meijere ('11) exhibit a Mendelian relationship to one another and are thus not in any way related to temperature nor to food-plant, particularly as all forms feed upon Citrus. Where there is an alternation of food plants it is evident that those of one generation must be primitive and those of the other more recently acquired, or else the insects in question originally fed upon all the plants concerned. The latter does not appear probable since the plants concerned are usually present at both times and it is difficult to see how any sort of memory of food-plant can be repressed in the first succeeding generation, later to be awakened in the second. Nevertheless, the behavior of the Tephroclystis appears to indicate such a temporary repression, if memory is concerned at all in the process of selection. The acquisition of new food-plants has actually been noted in a number of instances among various insects, as we have already seen.

The effect of hybridization on the selection of food plants by larvae of the first filial generation has been observed by Göschen ('13) in geometrid moths of the genus

Celerio. The European *Celerio euphorbiae* is represented by two subspecies or varieties known as *euphorbiae* and *mauretanica.* Both forms normally feed on Euphorbia and will not accept willow, but the hybrid *euphorbiae* ♀ × *mauretanica* ♂, known as *wagneri* and the reciprocal cross known as *turatii* both feed readily upon willow and can be raised to maturity upon it. Likewise, the hybrid *C. kindervateri* (*euphorbiae* ♂ and *gallii* ♀) feeds well on willow in the first generation of caterpillars, although *gallii,* like *euphorbiae,* does not naturally occur on any plants except Euphorbia, Galium and Epilobium. However, Schulze ('13) mentions several cases where isolated caterpillars of *C. euphorbiae* have been found on Polygonum, Syringa, Plantago and Solanum. Another instance in which Schulze reared upon willow a caterpillar found on Euphorbia is particularly interesting as this individual later grew to resemble *C. gallii* closely and probably represented a natural hybrid between the two species.

That hybridization does not always affect the selection of food-plants as has just been described is shown by some observations of Field ('10) on hybrid butterflies of the genus Basilarchia. In this case, three forms are concerned, *Basilarchia astyanax, B. arthemis* and *B. proserpina,* of which the last is considered for good reasons to be a hybrid between the first two. Field found that caterpillars produced by a *proserpina* captured in the open refused birch, poplar and willow, the preferred food of *arthemis,* but were successfully reared on wild cherry, one of the favorite food plants of *astyanax,* although the butterflies reared from them represented all three forms, *arthemis, proserpina* and *astyanax,* and he suggests on a numerical basis that they are derived from a *proserpina* (hybrid) × *arthemis* (color recessive) mating, especially as *arthemis* occurs commonly where the specimen was taken and *astyanax* does not. In this case the selection of an *astyanax* food-plant is quite unexpected and must be derived from an *astyanax* grandparent, although only one quarter of the butterflies reared from the brood of caterpillars proved to be *astyanax.* Unfor-

tunately, he was unable, on account of the impossibility of mating the butterflies in captivity, to study the food preferences of later generations.

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RESPIRATION AS A FACTOR IN LOCOMOTION OF FISHES

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THE accepted explanation of the locomotion of fishes not in contact with some solid surface is in terms of, first, the sinuous movement of the body, and, second, the movements of the various fins. The relative importance of the numerous factors embodied in these of obvious necessity differs from species to species, depending upon the degree and kind of specialization of any given form. While the present writer professes disagreement with the accepted explanations on several points as to the manner in which the known factors react on the surrounding element, it is not the purpose of this paper to attempt an overthrowing of these current conceptions, its purpose being simply that of calling attention to the existence of another factor in fish locomotion which had escaped the observation of students until discovered and called to my attention by Mr. Clifford M. Paxton of Brooklyn, New York.

Mr. Paxton has invented and claimed patent rights on a strikingly novel method of propelling ships which he calls an "induced stream line system." His thoughts, as developed, were the results of the contemplation of abstract hydraulic principles, but his discoveries and the developments of these principles caused him subsequently to conclude that fishes must receive locomotor benefit from the automatic operation of certain parts in accordance with one or more of the principles which he has developed for the high speed propulsion of vessels. A brief consideration of Mr. Paxton's propulsion method is necessary to a proper understanding of some of these newly discovered factors of fish propulsion.

The movement of a vessel is chiefly impeded by three obstacles, as described below:

(1) *Bow-wave:* When a ship is propelled through the water all the submerged surfaces of the entrance section are subject to the adverse pressure of the relatively stationary water which has to be forced out of the way to make room for the advancing hull. This water is projected away from the ship and represents lost energy. As the ship moves, other water has to flow in by gravity to fill up the space the hull moves out of. At low speed this is not a serious matter, as the water is moved slowly and has ample opportunity to readjust its level by gravity flow. At higher speeds, however, this is not the case and the water is "pushed and piled up" in the form of a bow-wave about the entrance portion of the ship.

(2) *Cavitation:* Likewise, in reference to the after portion of the ship, water can not flow fast enough in response to gravity to instantly fill in the space vacated by the ship, and there result hollows or "low pressure areas" about the run or after portion of the hull. These augment the retarding effect of the high pressure created forward to the end that there results a pressure differential with a large rearward component, which is the dominant limiting factor in the speed of ships.

(3) *Skin Friction:* The frictional resistance between the ship's surface and the water through which it is forced is given this term. While it is not a limiting factor and does not increase in the same ratio to speed as the pressure differential does, it is, nevertheless, an important item of resistance.

The first two of these resistance factors are as great or greater in the case of a submarine vessel (or a fish), although the adverse pressures are not ordinarily visible as waves on the surface.

With an apparently simple but nevertheless very ingenious arrangement of "developed" jets, Mr. Paxton has greatly reduced the retarding effect of these factors and at the same time has been able to develop sufficient reactive thrust to overcome the remnants of resistance that still remain. The invention has progressed beyond the theoretical stage, so the inventor's actual model will be described in lieu of a necessarily longer exposition of the abstract principles. This model is nearly an exact reproduction of a modern destroyer, Class 186, reduced to an overall length of thirty-four and one half feet on a scale of 1 to 9. On each side of the hull, midway between the waterline and the keel, a short distance aft of the bow a rearwardly directed nozzle is located, each having an orifice three and three twentieths inches long and five

thirty-seconds of an inch wide. They are so placed as to cause water expelled therefrom to sheathe the under-water hull a short distance aft of them, completely surrounding the hull at midship. The position of the intake orifice is of slight importance, usually being placed where most convenient and presented forward. At this point certain principles concerning the behavior of jets may be mentioned. Contrary to popular belief, the water set in motion surrounding a stationary submerged jet moves slowly in at right angles to the edge of the moving stream and then on contact passes along with it at a velocity only slightly inferior to that of the jet. This induced flow causes more water to move with it in a similar manner, and so on, thus spreading out the stream rapidly. The initial jet increases in sectional area by its deceleration to which is added the constantly increasing induced flow. Paxton finds that with jets of high velocity the cumulative stream as thus built up may be more than a thousand times the cross section of the initial jet stream. The truth of the foregoing has been satisfactorily demonstrated by experiment.

Another fact to be here noted is that a stream ejected along the side of a curved form will follow the contour presented, even if the curve is convex to the axis of the stream, provided it is not too abrupt. The stream does not veer off at a tangent as might be supposed, but closely follows the bending of the curve. With these considerations in mind the manner in which Paxton overcomes the three obstacles to the speed of vessels by his method may be considered.

Through the nozzles described he pumps a small quantity of water at a high velocity and neutralizes the three impediments to progress, as will be shortly described. This system of propulsion is not to be confused with many which have appeared from time to time that were based on nozzle reaction and used a large volume of water at comparatively low velocity with the orifice located elsewhere. All such have been proven to be less efficient than

the modern screw propeller. One important difference is that Paxton makes the lengths of the pressure reducing and pressure increasing portions of the jet stream correspond, that is, "fit," within limits, the respective lengths of the bow and stern sections of the hull.

(1) *Bow-wave:* This may be lowered slightly by a certain amount of water passing into the propelling system through the intake orifice, but this is wholly inconsequential, since possibly less than one half of one per cent. of the water moved away from the high pressure region forward is taken into the ship. The discharge nozzle slits are so located as to be in advance of the maximum pressure region and by virtue of the water movement induced by the sheet discharged through these slits the bow-wave is in practice actually eliminated.

(2) *Cavitation:* This posterior depression is filled by both the water ejected from the jets and the flow induced by them, so that the wake trends somewhat rearward instead of forward.

(3) *Skin Friction:* Considered as resistance to the ship's motion, this is largely overcome in that a considerable part of the frictional surface is transferred to the surface of the jet stream that sheathes the hull, for this may be considered practically as part of the vessel while it still follows the contour of it.

The ship as a whole reacts to the rearward movement of water about it and in addition there is the propelling effect of the nozzle reaction ample for any remnant of resistance. The reason for giving the jets a long narrow section instead of a circular one is for the purpose of placing a larger surface area in contact with the adjacent water and sheathing the hull satisfactorily; as well as concentrating the movement, reducing the time required for it, and making the jet stream "fit" the hull. According to Paxton the modern screw propeller is more efficient than his new method at very low speeds, but at relatively high speeds the relationship is reversed.[1]

Returning to the fishes, it should now be obvious that the water ejected through the gill clefts of typical Acanthopterygians is extremely similar in its effect to that of this new mechanical device that has actually propelled a model successfully. Experimentation has not been suf-

[1] All statements concerning his invention have been personally checked and approved as correct in a general way by Mr. Paxton, although naturally sketchy and inadequate for a full understanding of his invention as applied to ship propulsion. They are, however, sufficient for our purposes here.

ficient as yet to demonstrate just what locomotor advantage a given species may obtain from the water it ejects from its exhalent orifices, but the connection is evident and certain things have been proven which, together with certain indications, give food for some rather interesting reflections. An outline of the general trend of the writer's studies thus far is given below.

Recognition of the excellent but forgotten work of J. S. Brugmans is here made as he well recognized the possible importance of the influence of respiration on the locomotion of fishes. He, however, failed to comprehend the far-reaching significance of the reversal of pressure differentials and confined his thoughts to the simple reactive effect of the jets of exhaled water. His conclusion was that this effect was more important than any of the body and fin movements. No paper so far located since his time has even mentioned Brugmans' work or suggested independently the possibility of respiration having some effect on movement.[2]

An examination of over 300 diverse species of free swimming fishes taken at random (including both Teleosts and Elasmobranchs), most of which move at a considerable rate of speed, shows that over 90 per cent. possess gill clefts at a place which Paxton pronounces to be the theoretically correct position for the most efficient use of this method, as far as he could tell from available material, considering the varying forms. The remainder consist of few slight variations, none of which are large. Furthermore, even in sluggish forms the gill slits hold these positions fairly closely. It is only in such fishes that have progressed far from the typical ichthyized form that any wide variation is seen. Prominent among the latter are such highly specialized fishes as *Hippo-*

[2] Appreciation is here expressed to Miss F. La Monte, of the Department of Ichthyology, American Museum of Natural History, for translating the paper. "Aanmerkingen over de middelen door welke de visschen zich bewegen in het algemeen en over het vermogen der Uitademing tot dat einde in het bijzonder." Brugmans, J. S., Verh. l. Kl. Nederl. Inst. 1812, pp. 185–217.

campus, Histrio and *Lophius.* In the fast moving forms long, narrow, gill clefts are the rule, as typified by *Seriola, Scomber* and *Pomatomus,* while in the more sluggish forms small and often nearly circular exhalent pores are common as in *Spheroides, Balistes* and *Lactophrys.* Practically all intergrades are found between the two extremes which are beautifully correlated with other locomotor structures and known habits. Even in fossil fishes this correlation of the location of the gill clefts and the general body form holds good to such a degree that mere accidental association is out of the question. It is naturally difficult to obtain a measure of the force of exhalent water from living fishes moving at their higher rates of speed and at the lower rates perforce used in confinement, the body and fin movements which may be roughly analogized to a screw propeller have a great advantage. However, on the sluggish forms a definite demonstration of this force of the exhaled water is a simple matter, the Tetraodonts demonstrating it most clearly, although it must be admitted that here, on account of the rather wide divergence of the exhalent apertures, "nozzle reaction" plays a relatively larger part. Of these, *Chilomycterus schoepfii* (Walbaum) shows its ability in this direction better than any others so far examined. It is simply necessary to hold an individual of this species with its mouth immersed to observe this. Having little flexibility of body, it is unable to squirm about and necessarily confines its attempts to escape to violently lashing the caudal, anal and ventral from side to side and waving the pectorals about in addition to squirting powerful jets of water through the gill orifices. In a fish six inches long these jets may attain a height of considerably over two feet above the surface of the water. That these jets are of great use in locomotion there can be no doubt. In fact, specimens of this species have been seen to impel themselves forward through the water by this means alone at not much less than top speed. Besides being able to move themselves forward they have control of the ejections to such an

extent as to be able to effect turns by simply closing the proper aperture. If a sudden stop is desired they may close both valves and return the water through the mouth, but this is secondary to the brake-like effects of the pectorals thrown out at right angles to the axis of motion. A *Diodon hystrix* Linnaeus, with a length of about twenty inches, showed these same effects in a proportional degree, but on account of its inclination towards inflation was awkward to work with, although the results were more spectacular. It might be here called to the attention that submerged jets of pure water are perfectly invisible, and it is only when a suspended particle is acted upon by the jet that its force may be noted. Fishes that were held perfectly rigid so that there was no fin or body movement whatever appeared to be unable to eject jets with any force, simply respiring lightly, but as soon as the slightest tremor was permitted in the body the water was expelled violently. This suggests the possibility of a sympathetic nervous connection between the trunk and tail movements and respiration. Fishes of high speed, such as *Caranx* and *Seriola,* which could only be held with difficulty in a manner similar to that described for *Chilomycterus,* failed to respond appropriately, either flapping violently, or not respiring or if so only feebly, in such a manner that nothing could be deduced therefrom. The powerful *adductor operculi,* together with the branchiostegal rays and other compressible parts of the head, must make it possible for these species to eject water with a considerable velocity if so desired, and it may be mentioned that Paxton maintains that there is ample water ejected from fish held under such conditions to effect the purpose, the difficulty apparently being one of the velocity of ejection, which the musculature of the opercular and mandibular region could easily effect, were it not for some nervous inhibition incident to restraining the fish.

Probably the most satisfactory evidence in regard to these forms thus far obtained has resulted from the ob-

servation of specimens remaining quiet and freely suspended in the water. Various explanations have been given from time to time concerning the functions of the pectorals which usually are waved about rhythmically during periods of rest. The most generally accepted one being that it is done to maintain equilibrium, in that it is not done by fishes resting on the bottom. This theory has had the support of experimental evidence based on the removal of fins, it being alleged that fishes list to the side from which the fins have been removed and that with the removal of all paired fins the fish turns ventral surface up as a dead one.[3]

Repetition of these experiments failed to substantiate these statements as the results were directly in contradiction. Over a dozen diverse species (including these used by previous investigators) were experimented upon, varying between such extremes in form as the log-shaped *Esox reticulatus* (Le Sueur) and the deep, thin-bodied *Vomer setapinnis* (Mitchill), but the full results of the experiments will not be related here. Suffice it to say that whilst fishes with various combinations of paired fins removed were embarrassed in maneuvering in different ways, depending on what ones were missing, in no case was a disturbance of equilibrium obtained. As long as the individual remained at rest and attempted no turning or other maneuvering it retained the normal horizontal position.

A superficial glance at nearly any typical fish poised quietly in the water will convince any one that the pectorals are engaged in backing water. That is, the effective thrust is forward, which would tend to move the specimen in a backward direction. In connection with this newly described factor in locomotion it is conceived that the function of this movement of the pectorals is to neutralize the force of the exhaled water. It is not to be understood, however, that any considerable force is felt

[3] See R. C. Osburn, "The functions of the fins of fishes," *Science*, 1906, n.s. 23, pp. 585 to 587. Also the Cambridge "Natural History," Vol. VII, p. 353.

from the exhalations while at rest, as naturally the respiration is slower and furthermore the gill clefts are observedly cracked wider at such times, thus reducing the velocity of the emerging stream as well as increasing the cross-sectional area of it and consequently reducing both its velocity and surface area per unit of volume. The pectorals being usually placed directly behind the gills are enabled to intercept the stream and check the original direction of the thrust. The truth of these assertions is by no means simple to demonstrate owing to the large number of locomotor organs that generalized fishes employ either single or in numerous combinations, usually seven fins besides the body movements. In fact, it is rather seldom that fishes are seen free in the water with no apparent motion other than the pectorals. At such times they are seen to back water rhythmically and usually in perfect synchronism with the respiratory movements. That is, as the pectorals come forward the operculum lowers and forces the vitiated water out, the inhalation accompanying the return stroke. Usually, however, there are some other movements such as undulation of the dorsal or caudal as well as various others which sadly complicate matters so that it is a matter of patient waiting for a proper opportunity to see these two factors working together alone in direct opposition to each other. The removal of a single pectoral of a specimen of *Lepomis pallidus* (Mitchill) demonstrated this still further. On composure after release it backed water as usual with the remaining pectoral fin, but as the force applied was only one half of that previously used and on one side only, the fish moved forward, slowly curving toward the side possessing the fin. This motion appeared to disturb the specimen, causing it to speed up the number of oscillations. As now the force of the fin overcame that of the jets the fish moved slowly backward and curved slightly to the opposite side. In a short time the fish learned to compensate for the missing member by waving the posterior tip of the soft dorsal which it bent

towards the side of the missing pectoral, and from then on had no difficulty in maintaining any position desired. Most of the Centrarchidae use either or both median fins in this manner occasionally, making the learning of this accomplishment no new feat. On this account also it is usually done by specimens practically immediately on coming to rest. The particular individual described above probably represents a slight subnormality in nervous adjustment.

Even ignoring these experiments it is still indisputable that any jet expelled from a floating body must tend to move it in an opposite direction, if simply by plain reactive force as Brugmans clearly indicated; so, when such other factors enter as the reduction in resistance, as mentioned previously, it is reasonable to suppose that the actual thrust obtained would be of some practical value to ichthyized forms. It is almost needless to add that while fishes below the surface do not throw up a bow-wave or dig out a cavitation behind, the differential pressure areas have identical effects, but are not ordinarily visible as but a single medium is involved. The reduction of skin friction is probably negligible in fishes on account of their effective mucous coat, but the other two and more important obstacles to speed must be overcome by muscular action.

Looking at the question from a phylogenetic standpoint there seems to be no very good reason why the port of exhalation in such diverse animals as Elasmobranchs and Teleosts should have such a community of placement, unless there is a positive advantage to be attained by so placing them or a definite disadvantage in having them placed anywhere else. To assume the latter is simply to euphemize the former, for as we have shown in the previous paragraph any jet of such nature must have its reactance, however slight. If there was not some sound advantage in ejecting water forcibly it would seem a useless expenditure of energy on the part of many fishes while swimming to pump water in and out when

by simply opening the mouth a greater amount would flow over the gill membranes as long as the fish moved forward because the flow would not be intermittent. Actually, this has been observed in both *Carcharias taurus* Rafinesque and *Anisotremus surinamensis* (Bloch) when swimming leisurely. Furthermore, fishes which might be expected to make excellent use of this simplified manner of breathing, such as many members of the Carangidae and Scombridae, have particularly well-developed opercular apparatus.

Respiration thus further complicates the study of the functioning of the remaining factors as the reaction of any fin or body movement is so modified that the effective thrust is the resultant of such and the respiratory effect, and as the respiration of fishes is an intermittent process it is clear that their mechanism would not be as efficient as a machine giving continuous flow. The resultant reaction would depend on whether inhalation or exhalation was taking place at the moment of a given fin or body movement. The exhalation of fishes is not to be confounded with the simple reactive jets of the so-called Syringograde animals which suck up water slowly and expel it with violence through the same or a nearby aperture, such as the Cephalopods, Medusae and certain Odonata nymphs. This notoriously inefficient method may be compared to the discredited jet propulsion systems of the past.

In the light of this evidence the question is no longer concerned with whether or not fishes in general receive a perceptible thrust from the exhaled water, but resolves itself into detailed study of the amount of its locomotor function for each particular species.

THE MAXIMUM SPEED OF FRESH-WATER FISHES

EMERSON STRINGHAM

THE question of the speed with which fish swim has elements which it would seem might make it popular, but there appear to be few recorded observations. It becomes of economic importance in connection with the effect of water power development on the fisheries. Against what velocity of water in a fishway can a fish ascend in order to go through the fishway, thus getting above the dam? Against what velocity can it swim up a tail race of a power house, where it might be injured by the water wheels?

The evidence consists, in part, of measurements of the velocity of water through which the fish swim. It may be safely inferred that a fish can swim a little, but not much, faster than the speed of the fastest water it is able to swim against.

An observer who has given no particular consideration to the matter might infer from the fact that fish go up rapid streams that they are able to swim continuously against such water velocities. The movement of the water of a stream is, however, very complex. At the surface there is a retardation by the atmosphere, and at the bed of the stream a greater retardation by the solid soil or rock, this retardation by the bed becoming very pronounced when the bed is unusually rough. Behind, and even on top of obstacles, the water may be nearly still while it is rapidly racing by on all sides. And at places there are eddies, even of substantial area, where the water at the edge of a stream flows in the opposite direction to that in the main channel. The author noticed a striking illustration of this below the Great Falls on the Caney Fork River, Tennessee, where floating objects traveled in an orbit at the edge of a raging current; simi-

larly, in a fishway at East Taunton, Massachusetts, there were places where the water doubled back, and the fish maintained themselves by directing their heads down the fishway. The United States Geological Survey have published extensively on the subject of stream flow; a paper by Pierce (1916) contains interesting data on the retardation of flow at the bed of a rapid current. These irregularities, furnishing helpful countercurrents and rest pockets, make it possible for fish to ascend streams that would otherwise stop them.

A Belgian engineer (Denil, 1909, pp. 33–34) has emphasized the distinction between a sudden bound and ordinary swimming. This distinction, in common with the generality of distinctions, must be regarded as relative rather than absolute, but none the less useful on that account. There would certainly be found all intermediate rates between the sudden bound and the slowest movement. The same authority recognized two sorts of bounds, that into the air and that through the water; with the former we are concerned only so far as it is evidence of velocity in the water. He reports having personally seen a large number of salmon force themselves by a distinct effort through several meters of water, of which careful measurement showed the mean velocity to be 5.00 meters per second. This represents a speed of slightly over 11 miles an hour.

Computations made on the basis of the height that a salmon rises above the water give a higher figure.[1] Day (1887, p. 73) concludes that six feet is probably as much as a salmon under ordinary conditions could accomplish. According to elementary mechanics the initial velocity of a body ascending vertically against gravity equals the square root of twice the product of the force of gravity into the height of the rise, or

$$v = \sqrt{2gs}.$$

Taking g as 9.8 meters, and s as 2 meters (about $6\frac{1}{2}$ feet), the initial velocity would be not quite 6.3 meters a

[1] This method of attacking the problem was suggested by Mr. A. A. Doolittle.

second. In fact, the fish leave the water not vertically but at some angle to the vertical; therefore, the initial velocity would equal the product of the secant of this angle into $\sqrt{2gs}$. If the angle be taken as 45° the secant is $\sqrt{2}$. Indicating this initial velocity by v′,

$$v' = \sqrt{2} \times \sqrt{2gs} = 2\sqrt{gs} = 8.8+,\text{ for the assumed value of } s.$$

This gives the velocity in meters per second; the equivalent value in English measure is 19½ miles an hour.

The same author (Day, 1887, p. 73) mentions reports of higher leaps which would give initial velocities of 10 meters a second or, if made at an angle of 45°, 14 meters a second.

For the benefit of those who observe fish jumping but have no special interest in mechanics the following rules are stated:

Let "m" be the height of the leap in meters measured from the highest point attained straight down to the water, and "f" be the same in feet, then

The initial velocity of a fish leaving the water perpendicularly equals $4.4\sqrt{m}$ in meters per second, or $8.0\sqrt{f}$ in feet per second.

The initial velocity of a fish leaving the water at an angle of 45° equals $6.3\sqrt{m}$ in meters per second, or $11.3\sqrt{f}$ in feet per second.

The initial velocity of a fish leaving the water at a smaller angle to the vertical would be intermediate in value between these two, and can be computed by the general formula hereinbefore derived.

The conclusion of Denil (1909, p. 34) as to more sustained effort by the salmon is that they may be expected to swim against a current of 3.15 meters a second for at least 14 meters. This figure is in close agreement with an opinion expressed by Napier (1914, p. R 40):

. . . it is well to point out the capabilities of the average sockeye observed under various circumstances. A vertical jump from still water, 1 foot or more deep, to running water above is certain under a height of 18 inches, and probable up to a height of 3 feet—a forward jump is generally uncertain. The fish can travel without rest for about 10 feet up a current of five miles per hour where the stream-line of that current is steady.

A passage can be effected up a shallow cataract 3 feet long and 1 foot high. Within limits, the direction and not the velocity of a current is the determining factor with regard to the difficulty of any passage. A sockeye

is apparently unable to pass, even from still water, a rectangular obstruction of 2 feet side with sharp edges whose up-stream face is flat and placed square to a current of five miles per hour or more.

It is possible, however, for a fish to pass an obstruction of similar size under the same conditions if the obstruction is waterworn and the edges are sufficiently rounded. Apparently these sockeye are able to pass conveniently up a current of five miles per hour when the force of that current is tending to hold the fish against a rock-face, if slightly irregular or against a slope of broken stone, when the angularity and size of the stones are, broadly speaking, inversely proportional.

The limiting velocity of a steady stream up which a sockeye is apparently capable of swimming lies between six and seven miles per hour, but only for very short distances, though a slight up-draft may help or hold a fish steady for a few moments.

A French engineer (Lavollée, 1902, p. 289) found that salmon of ordinary size appeared to find the limit of their strength in a current with a mean velocity of about 3 meters a second. In the opinion of von Bayer (1910, p. 1044) fishways, of the pool and fall or counter current types, should have a current velocity not exceeding 10 feet per second.

During a discussion of this subject at the Biological Society of Washington (D. C.) on January 26, 1918, Mr. Vernon Bailey told of spearing pike when he was a boy, and that he was able to run as fast as the pike could swim. A boy could probably run 8 or 10 miles an hour under these circumstances. Another member of the audience told of similar experiences with black bass and eels.

In the spring of 1917 the writer had an opportunity to study several fishways in Massachusetts, and to make some observations on the velocity of water up which the fish swim. These fish were *Pomolobus pseudoharengus* (Wilson), one of the common alewives. The instrument used to measure the velocity of the water was a Price penta-head meter, belonging to and calibrated by the United States Bureau of Standards. The table accompanying it showed the number of revolutions for velocities up to nine feet per second, but some of the measurements ran considerably above this. To get an approximate idea of what these velocities were the data supplied were plotted on cross-section paper, and a curve drawn through the points and extended freehand. For this rea-

son observations on velocities of more than nine feet per second are less dependable than the lower ones.

Of the places visited three yielded observations bearing on the question under consideration. At East Taunton the fish were freely using a small fishway, at least 180 of them passing out at the upper end in the course of half an hour. Measurements were made of the rate of flow at seven points in the fishway where the current appeared to be greatest, and it was found to vary from four to five feet per second. At Middleboro the fish were, on the day of observation, unable to ascend a little sloping falls where the velocity was about 11 feet per second. Just below they were swimming through one place where the current was 5.3 feet per second. At East Wareham the head of water, and therefore the velocity, could be varied. The fish swam up a slope about three feet long where the water was going down at rates of 6.1, 7.8 and even 9.8 feet per second. They were perfectly helpless when it was raised to 13½ feet per second. At one place where the water was very shallow they failed to get up against a velocity of 9.3 feet per second. While this species sometimes jumps at least part way out of the water, they swam through the velocities here mentioned.

The indicated velocities for swimming, as distinguished from bounding, may be included in one table as follows:

SWIMMING SPEEDS IN MILES PER HOUR

Lavollée	*Denil*	*Bayer*	*Napier*	*Bailey*	*Stringham*
salmon	salmon	....	salmon	pike	alewife
6¾	7	6.8	6 to 7	8 to 10	6.8

These figures are in good accord for the medium-sized freshwater fishes, except in the case of the pike. The speed noted for the pike is perhaps to be regarded as that of a bound or jump, rather than that of swimming. For the alewife, however, the speed of 6.8 miles per hour was also for very short distances and is, perhaps, the bounding rather than the swimming speed.

The large marine fishes and mammals present a wholly different problem. It has been found by different observers (Hecht, 1916) that for eleven species of fish the

weight is equal to the cube of the length multiplied by a constant, the constant varying with species and season. If, now, the motor energy increases in general with the weight, it is quite possible that the locomotive force is a function of the third power of the length, while the resistance to be overcome increases only as the second power. Should this be the case it would explain why the speed of sharks and porpoises, observed from steamers, is so much greater than that of the little fishes of the rivers. If, on the other hand, fish like the mackerel attain these high velocities, other factors must enter.

For the medium-sized fresh-water fishes the maximum swimming speed appears to be about seven miles an hour, with the possibility of a bound at nearly three times this rate. More detailed observations will be needed to show variations with species, sex, water temperature, physiological conditions and so on.

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DO ANESTHETIZED BEES LOSE THEIR MEMORY?[1]

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There seems to be a widespread belief that hivebees, unlike vertebrates, lose their memory on being anesthetized. Von Buttel-Reepen,[2] one of the foremost German bee students (p. 163), has the following to say concerning this question: "Betäubt man Bienen mit Salpeterdämpfen, Äther, Chloroform usw., so verlieren sie ihr Ortsgedächtnis. Während die Bienen sonst—innerhalb des gewöhnlichen Flugkreises auf einen anderen Platz versetzt—auf die alte Stelle zurückfliegen, so benehmen sich betäubt gewesene Bienen anders, sie bleiben im allgemeinen dort, wohin sie gebracht werden und fliegen nicht wieder an die alte Stelle zurück, sie vergessen das frühere Heim." A similar view is expressed by Dr. E. F. Phillips,[3] of the United States Department of Agriculture, in his discussion of memory in the hivebee. Dr. Phillips (pp. 179–180) says: "The best evidence of memory is found in the fact that memory is sometimes lost. If bees are stupefied by tobacco smoke, by the smoke of the puff ball (an old practice) or by some anesthetic, they are unable to return to their old location and must re-orient themselves after they revive."

During the latter part of the summer of 1922, Dr. W. M. Wheeler, of the Bussey Institution, suggested that the writer anesthetize a colony of bumblebees in order to see whether they are affected in the same way as hivebees. On September 11, 1922, a colony of *Bremus* (*Bombus*) *impatiens,* consisting of the old queen, 18 young queens,

[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 228.

[2] Das Leben und Wesen der Bienen. Braunschweig, 1915.

[3] Beekeeping. The Macmillan Company, New York, 1921.

about 200 workers and a considerable quantity of brood, was discovered in the Arnold Arboretum, about half a mile from the grounds of the Bussey Institution, and this furnished an excellent opportunity for carrying out Dr. Wheeler's suggestion.

Experiment I

In the forenoon of September 12, 1922, all bees present in and about the above-mentioned nest were captured and placed in a glass jar, whereupon both bees and comb—the latter in a separate receptacle—were taken to the Entomological Laboratory of the Bussey Institution, where 100 workers and 5 young queens were etherized and marked (on the dorsal side of the thorax) with white ink. At 11 a. m., both the etherized and the non-etherized members of the colony were taken to the Bussey Bee-yard and transferred to an open observation-box containing their comb. When the old nest-site in the Arnold Arboretum was visited about 1.30 p. m., a large number of workers, including many marked individuals and two of the five marked queens, were found on or near the nesting-material which had been left in the nest-cavity.

Experiment II

About half an hour later, twenty of the marked workers which had returned to the old nest-site were recaptured and taken to the laboratory where they were again etherized and marked—this time on the dorsal side of the abdomen—whereupon they were returned to their comb in the bee-yard. When the old nest-site was visited at about 5 p. m. that afternoon, six[4] of these twenty marked workers were again found on or near the nesting-material.

The results of these two experiments showed clearly that etherized bumblebees do not lose their memory and that etherization has a similar effect upon them as upon vertebrates. With this fact established, it seemed strange

[4] As in the preceding case, several of the etherized bees failed to revive

that anesthetics should have a different effect on hive-bees, and the writer, therefore, decided to test the correctness of the two statements which were quoted at the beginning of this paper. In order to make this test, it was necessary to secure the services of a second person, and the writer here wishes to avail himself of the opportunity to thank Messrs. Albert and Theodore Mangelsdorf for their generous assistance in connection with the following experiments.

Experiment III

On July 8, 1923, at about 4 p. m., twelve drones and twelve workers (field bees) of *Apis mellifica* were captured in front of hive No. 1 and etherized, whereupon they were marked with white ink. After most of them had revived, they were transferred to a place about one tenth of a mile from their hive and liberated by Mr. Albert Mangelsdorf, while the writer was stationed at the hive entrance. The results of this experiment are shown in Table I.

TABLE I

Number of bees departing from place of liberation.[5]	♂	☿	Time	Number of marked bees entering hive.	♂	☿
2	1	1	5.21 P. M.	0	0	0
2	0	2	5.22 " "	0	0	0
0	0	0	5.23 " "	1	1	0
0	0	0	5.24 " "	1	0	1
0	0	0	5.29 " "	1	0	1
1	0	1	5.30 " "	0	0	0

At 5.29 p. m., one of the two marked workers which had returned, again left the hive and it therefore seemed best to discontinue the experiment.

Experiment IV

This experiment was carried out in the early part of the afternoon of August 5, 1923. Because of difficulties

[5] At 8.30 P. M., about half of the bees used in this experiment were still crawling about aimlessly near the place at which they were liberated. They were still so dazed that they were unable to fly even when thrown up into the air.

in capturing field bees, thirteen workers which were guarding the entrance of hive No. 2 were etherized. In this state they were taken to a place about one tenth of a mile from their hive, where they were marked and placed in a box containing freshly-gathered honey. After most of the bees had revived, they were transferred to a shady place about one eighth of a mile from the bee-yard and liberated at 2.20 p. m. by Mr. Theodore Mangelsdorf, while the writer was again stationed near the hive entrance. By 2.44 p. m., all the bees but one (this one failed to revive) had departed, but up to 2.45 p. m. none of them, so far as could be determined,[6] had returned to the hive. Professor Z. P. Metcalf, of North Carolina State College, who was watching the progress of this experiment, examined several of the bees used and found them to be young individuals which had probably never left the hive before, a fact which no doubt chiefly accounts for the negative results of this experiment.

Experiment V

On the same day (August 5, 1923) at about 3 p. m., twenty-five field bees were captured in front of hive No. 3 and etherized. In this state they were taken to the laboratory where they were marked with white ink and placed in a box containing a small piece of comb honey. About two hours later, they were transferred to the Bussey Dormitory, about one eighth of a mile from their hive, and liberated from a second story window by Mr. Theodore Mangelsdorf, while the writer, as in the two preceding experiments, was again stationed at the hive entrance, this time provided with veil and gloves. The results of this experiment are shown in Table II.

[6] The writer had failed to provide himself with a veil, and the capture of bees in front of their hive had so enraged certain members of the colony that they resented his presence with telling effect. It is possible, therefore, that the return of some of the marked bees may have been overlooked.

TABLE II

Number of bees departing from place of liberation.	Time	Number of marked bees entering hive.
7	5.20 P. M.	0
2	5.21 " "	0
2	5.22 " "	1
1	5.23 " "	0
3	5.24 " "	1
2	5.25 " "	1
0	5.26 " "	4
1	5.27 " "	1
0	5.28 " "	1
0	5.29 " "	0
1	5.30 " "	1
0	5.31 " "	1

At 7.45 on the following morning, two of the bees used in this experiment were still crawling about in a dazed condition near the window from which they had been liberated, showing that bees, like human beings, exhibit great individual variation in their resistance to anesthetics.

The results of the foregoing experiments seem to warrant the following conclusions:

(1) Neither bumblebees nor hivebees lose their memory on being etherized, and hence are able to return to their nests or hives, provided they are in good physical condition and have not been kept under ether too long.

(2) The statements of von Buttel-Reepen and Dr. E. F. Phillips are probably based on experiments in which many of the bees were killed[7] by the anesthetic, or so enfeebled that they died prematurely, while others were perhaps unable to fly for a considerable period as a result of the ordeal.

These conclusions also seem to be supported by the behavior of the pomace-fly (*Drosophila melanogaster*). As every geneticist knows, this insect retains its instincts (inherited memory) even after repeated etherization.

[7] This fact may be easily overlooked, if a colony of bees is anesthetized in the hive.

A CASE OF COMPLETE SEX-REVERSAL IN THE ADULT PIGEON

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I

INVESTIGATIONS conducted during several years on the general problem of sex, and on the nature and control of sex in particular, have made it relatively clear and practically certain that the sex of numerous pigeons has been reversed in the earliest (gamete) or egg stage. In these cases the difficulties confronting the competent investigator do not so much lie in effecting the sex-reversal as in the two following aspects of the problem: First, in obtaining for others the kind and amount of crucial data for each of a large number of cases of complete reversal, and for other numbers of less complete reversal effected by the same means. And second—since the reversals are made in both directions—to find, isolate or measure the common element involved in the change of female gametes to male zygotes, and of male gametes to female zygotes. These two tasks, we believe, now face more than their inherent difficulties because of some widely accepted assumptions concerning sex which seem largely to partake of the value of facts in the minds of many geneticists—particularly among many leaders on the zoological side of this new science.

In contrast with the relatively large numbers of experimentally induced cases of sex-reversal obtainable in the egg-stage, we can expect only small numbers of proved cases of "naturally" occurring complete sex-reversal in adult birds. This follows from the already evident circumstance that this type of reversal will probably occur only in those adults which develop special diseases in particular or restricted organs. And within this selected

group it is only in those individuals which check the disease, return for at least a short period to a fair state of health after the injury or destruction of the gonad, and also further escape destruction at the hands of their owner during this long period of "uselessness," that complete sex-reversal in the adult can be accomplished.

Not many such highly selected individuals, with the requisite well-recorded history of their sex-performance in the first sex-stage, will come under the observation of the prepared investigator. Even then the gauntlet is not yet run and the case may still fail to be recorded as sex-reversal. If the investigator should decide to kill his bird before the reversal was quite complete, or if he be quite saturated with assumptions concerning a cytological foundation for hermaphroditism in birds, he would find it practically necessary to describe the case as one of "hermaphroditism." Though proved cases for the adult must probably long remain relatively few in numbers, one apparently adequate case has just been described in the fowl, and we here wish to add another from the pigeon. Even with these two cases we may hope to break down some of the assumptions to which reference has been made, and thus later obtain a fairer field for the examination of the evidence for the more numerous sex-reversals in the egg-stage.

II

Crew[1] has recently described a case in the fowl which he rightly considers the most clear-cut instance of sex-reversal in (adult) vertebrate animals yet recorded. From the owner he obtained a Buff Orpington hen 3½ years old. According to what he evidently considers unquestionable evidence given by the owner this hen had produced eggs and had hatched young from them before ceasing to lay at slightly over three years. When first brought under the observation of Dr. Crew at 3½ years this hen was still a nearly normal hen in appearance, but

[1] Crew, F. A. E., *Proc. Roy. Soc.*, B, 1923, *95*, 256.

was developing a tendency to crow. During the 22 months this bird was under Crew's observation her comb notably enlarged, she developed spurs from the merest rudiments to a length of 4 and 5 cms; she assumed the plumage, copulatory and fighting behavior of a cock, produced live sperm, fertilized two eggs of a virgin Buff Orpington hen and thus became the father of two young—a male and a female. These latter "were inter-bred and their progeny are typical Buff Orpington chickens."

The autopsy of this fowl—made after this bird again became sick, though dead of accident December 29, 1922 —revealed very extensive abdominal tuberculosis, in which an enormous liver (340 grams), the gizzard, intestine, peritoneum and ovary were involved. The oviduct had almost disappeared and two vasa deferentia were present. Two testes ($3\frac{1}{2}$ x 2 cm) with even outlines and surfaces were found. A complete account of the histology of the nearly destroyed ovary and of the two testes has been separately given by Fell.[2] Crew discusses the condition of this bird after she ceased laying in the following terms:

> In the autumn of 1920 she began to suffer from ovarian disease, which became noticeable in January, 1921. The disease was tuberculosis of the ovary, which progressively removed the ovarian tissue and so produced the effects of pathological ovariotomy. But it would seem that this tumor growth in its effects *so altered the general metabolism* (italics are ours) of the individual that the conditions favorable to the differentiation and growth of spermatic tissue were created. New sex cords developed from the germinal epithelium and spermatic tissue was differentiated both in the left gonad and also in the incompletely atrophied right.

Among the seven additional cases of more or less masculinized hens described by Crew there is one additional case in which the histology of the gonads revealed both ovarian and testicular tissue and for which the former owner of the bird states that eggs were previously laid. The other six cases showed one or another admixture of ovarian-testicular tissue, but there is no previous history of egg-laying. All the eight cases are interpreted by

[2] Fell, H. B., *Brit. Jour. Expl. Biol.*, 1923, *1*, 97.

Crew and by Fell as "hens at various stages of sex-reversal" and "in every case the development of testicular tissue was preceded by ovarian atrophy or disease." It may be further noted that there can be little doubt that most of the cases of so-called "hermaphrodites" described in birds by Tichomiroff,[3] Brandt,[4] Shattock and Seligman,[5] and several more recent observers, were in reality cases of incomplete sex-reversal. Also, that in spontaneous reversal from female to male the development of testicular tissue frequently, perhaps always, follows a tuberculous infection and destruction of the ovary.

III

The facts and details of the case observed by us may next be presented. On January 15, 1914, three pairs of presumably healthy blond ring doves were obtained from Mr. John N. Johnson, who had reared them and a few other birds at the Station for Experimental Evolution in addition to his duties as caretaker of animals at the laboratory. One pair of these birds bore leg-bands, and it thus fortunately happened that the two birds of interest to this presentation were provided with numbers wholly unlike all other numbers utilized before or since in our own breeding work. These numbers were: 16,588 and 16,580. It is not possible that either of these numbers was misread at autopsy. These two birds were said to be adult when obtained and were probably the parents of the pair of immature young obtained along with them; but this point is immaterial, since the tabulated data show that other eggs were laid 12 days after the pair was in our own care.

These two birds were given a pen separate from all other birds on January 15, 1914. Eleven eggs were produced within the following 90 days. These birds were believed to be pure blond rings, and it was decided to study the yolk size of all eggs laid. The hour of laying

[3] Tichomiroff, A., *Proc.* Nat. Hist Soc., Moscow, 1887, *52*.
[4] Brandt, A., *Zeit. f. Wiss. Zool.*, 1889, *48*, 101.
[5] Shattock and Seligman, *Trans.* Path. Soc. Lond., 1906, *57*, 69.

was recorded for every egg laid and No. 16,580 was identified as the layer of these eggs. The remainder of the recorded history of this female is given in Table 1, and the remarkable record of her body weight and of its changes during a three-year period are given in the curves of Figure 1.

The data of the table leave no doubt that ♀ 16,580 laid eggs during three months at the beginning of 1914. Also that at this time this bird was not able to produce a pair of eggs within less than 9 days following the last egg of a preceding pair. This is a strong indication that the ovary of this bird was not then in a vigorous state; for long experience has shown that when the ovary of birds of this species does not lag in starting a new pair of eggs on their last growth cycle the next following egg is laid at 7 days after the previous clutch. An ovarian lag of 2–15 days was shown in each of the five instances tested. A further indication that something was wrong in the ovary of this bird, even at the time of laying this series of eggs, is found in the abnormal size difference of the two yolks of pairs D and F.

After the eggs of April 13–15 were laid it was necessary to give to this pair the eggs of other birds to incubate and rear. The record shows that these eggs were hatched and the young deserted within a week. Twenty-five days after these young were removed the female took her nest as usual for laying, but no eggs appeared! She and her male mate had manifestly gone through the time, copulations, etc., necessary for the production of eggs and both incubated normally; they were given eggs of other birds and successfully hatched and reared these young. This performance was later twice repeated during 1914, and from April to September of the following year was several times repeated. These failures to produce eggs point definitely to disease of ovary or of oviduct, or of their disappearance, during these periods.

Prior to February 1, 1915, it was realized that although these birds were vigorous and continued to copulate they

had for long produced no eggs. They were therefore brought into another building, where studies on sex behavior were being conducted daily, and so placed that we might more often observe the activities of this laggard pair. It soon developed that this female was usually and frequently forcing her *male* mate to function as a female in copulation. This was 10½ months after the female had laid her last egg. The pair continued to incubate without producing eggs, and 18 months after her last egg No. 16,580 was found to have developed the coo or crow of a male.

On May 28, 1916, after 6 weeks of complete idleness, this pair was removed to another building and placed with a small group of other spent and worthless ring doves. Six weeks later the emaciated male died and the weights and measurements of his testes were obtained. It was 17½ months after the death of the male, and 44½ months after the time of the laying of her last egg, that No. 16,580 died with very advanced tuberculosis.

The death occurred and the autopsy was made on December 29, 1917—just 6 years ago. On the evening of this same day the writer, after personally making the autopsy, left his laboratory to attend the annual meetings of the scientific societies then being held in Pittsburgh. Only upon his return, when it was too late to recover the discarded testes for sectioning, was it learned that this autopsy was that of the former female—not that of the *male* as supposed at the hour of autopsy—of this pair of birds. Failure to photograph or to section these testes, and thus make it possible to give to others this evidence of the final maleness of the bird, does not affect the conclusiveness of the demonstration of a complete sex-reversal. To one at all familiar with the gonads of pigeons the confusion of testis and ovary is incredible. We have indeed met with mixed and doubtful cases, but these have all been questioned and generally preserved for microscopic study.

The lack of photographs or of sections of these par-

ticular testes nevertheless persuaded us to reserve this case for presentation in connection with a complete account of our sex studies. It was thought that the reader would then have better opportunity to judge of the detail and accuracy of our work in general and thus be brought to share our conviction of the impossibility of error in this case. Crew's publication, however, now fully covers the gonad histology of a quite parallel case in the fowl, and further clears up much concerning the place and method of origin of testicular tissue within diseased and disappearing ovary. Again, our own case usefully supplements that of the fowl, since we obtained accurate data on the egg-laying history, while this part of the record for Crew's case is at least differently covered—by the credible word of the former owner, by the earliest competent records on external appearance, by the succession of changes in appearance, and by the final identification of disappearing ovarian tissue.

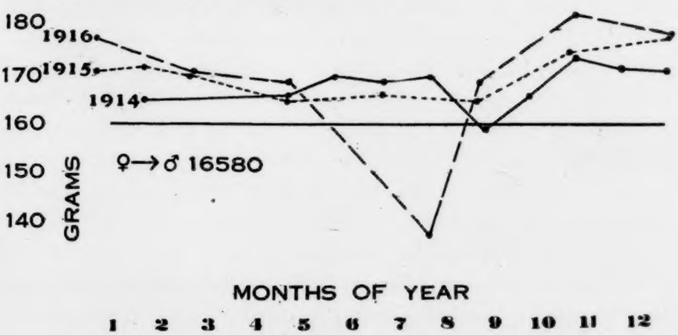


FIG. 1. Curves showing body weight of ♀ → ♂ 16,580—1914 to January, 1917.

The curves for body weight, formed from weights of No. 16,580 taken at various intervals between February 3, 1914, and January 5, 1917, are worthy of examination. During neither of three years covered by the data, do the seasonal fluctuations of the body weight approach the normal. During 1914 her weight either increased or remained high from May to August. This is the period

during which this bird lost her capacity to produce eggs; and it is the season during which body weight normally shows a decrease, attaining its minimum in September (actually attained here) or October. The amount by which the autumn weight (September) is decreased from that of February and May is both too slight and of too short duration. The curve for 1915 shows that when the bird's weight should have been lowest, in September or October (when bird began to crow as a male), it was equal to or greater than that of May. The 1916 curve shows an extraordinary loss of weight (23 per cent.) from January 3 to August 3 and a still more extraordinary gain (34 per cent.) between the latter date and November 3—this increase occurring at the season when the weight normally decreases.

Other general facts recorded in the curves are also notable. The body weight is higher than that of a normal female during all three years, and was most nearly that of a normal female during the actual period of egg-laying. The winter weight, and indeed the average yearly weight, was progressively greater with each succeeding year. Excepting only the period during which eggs were laid the body weight throughout is more nearly that of a normal male (about 170 grams) than that of a normal (about 160) female. The bearing of all this on metabolic changes in this bird is obvious.

The fact that the left testis of No. 16,580 was larger than the right is important. The general significance of this condition in pigeons was reported[6] several years ago. We then presented evidence that this is a reversal of the normal size-relation of the two testes, and "that a male which is forced to arise from a female-producing egg may (thus) show in the relative size of its gonads an approximation to the relative size of the gonads of a female." Likewise, in the present case the larger left testis reflects the earlier femininity of the bird.

[6] Riddle, O., *Anat. Rec.*, 1918, *14*, 283.

IV

The cases of complete sex-reversal in the adult pigeon and fowl are each accompanied by data which make it possible and profitable to consider the mechanisms involved in these cases of sex-reversal. In our consideration of this important aspect of the problem we are led to conclusions differing in some respects from those of Crew. To us it is obvious that a satisfactory conclusion must take cognizance not only of both these cases of adult sex-reversal, but of all other established facts of sex and the modifiability of sex. At the outset, however, it can be said that our case and all other established facts known to us agree with Crew's conclusion:

> The type of sex-organization and of the reproductive functioning of the individual are not irrevocably decided by the sex-chromosome constitution. It is certain that an XY individual—a "determined female"—can produce sperms just as efficiently as it can produce ova. . . . The transformation of the sex organization of an individual, a determined male or a determined female, into that ordinarily possessed by an individual which has the alternative sex-chromosome constitution is an established fact.

My own conclusions, and their divergence from certain other of Crew's conceptions can not be presented fully here. In general, however, our views concerning the present data are quite the same as those stated in our several publications of the last twelve years—the case here described having been available to us during the last six years. It is not practicable, however, to give here a full discussion of all aspects of these two cases.

The history of these two special cases of sex-reversal indicate to us that the transformation of these adult female birds into males was associated with the same general principle which we believe we have fairly established in our earlier studies, namely, that those conditions or agencies which *increase the metabolism* of gamete or zygote tend to carry development in the male direction. With this principle[7] in mind one may then

[7] Another principle which probably applies to these cases, but which for practical reasons can not be discussed here, is the following: In birds specifically and probably in vertebrates generally the males carry the ontogenetic development of characters associated with sex to a further (phylogenetic) point than that attained in the females.

consider the evidence that tuberculosis in particular, and the destruction of the ovary in general, may effect such an increase of the metabolism.

There is of course obvious evidence that the metabolism of the tuberculous individual is increased, and quantitative data for the human are available (see Cordier).[8] The related facts then indicate that the two described cases of complete sex-reversal—fowl and pigeon—both changed from female to male, and this change was simultaneous (or certainly nearly so) with a change from lower to higher metabolism. In these two cases, however, there was not only tuberculosis in the organism, but a tuberculous *destruction* of the *ovary*. Probably it is only in this latter case, where the defense of the ovary for its own maintenance are largely or wholly removed by disease, that complete sex-transformation can occur in adult birds.

Tuberculosis in organs other than the ovary has also been found by us to accomplish the partial masculinization of the female pigeon. For many years we have recorded case after case of female ring doves which stopped laying, ceased showing female behavior, and later attempted to copulate as *males* with their male mates. At autopsy such birds have in most cases proved to be tuberculous. Tuberculosis induces a higher level of metabolism, and in all these cases the changes are from females to or toward maleness. Metabolic level is the common factor for these, and the numerous cases of sex-reversal in the gamete stage in the pigeon. In some of our earlier studies[9] we have specifically dealt with the applicability of this same factor to the other several known cases of modification of sex in animals. Further, during the past 12 years we have presented parts of our accumulated evidence that this same difference in metabolic level characterizes the male- and female-producing *gametes* in the pigeon. This has carried the earlier con-

[8] Cordier, V., *Compt. Rend. Soc. Biol.*, 1923, *88*, 782.

[9] Riddle, O., *The Amer. Acad. of Med.*, 1914, *15*, 265; AMER. NAT., 1916, *50*, 385; *Science*, N. S., 1917, *46*, 19.

ception of Geddes and Thomson into quite new territory.

In another communication[10] we have shown that among ring doves the ovary is much more frequently the seat of macroscopically observable tuberculosis than is the testis. There and elsewhere[6] it was also shown that active and progressive tuberculosis in other organs is associated with atrophy of the testis. This well-established observation makes it wholly probable that after tuberculous destruction of the ovary, the bird must check the active progress of tuberculosis in the organism in order that a fully functional testis may be formed.

We have earlier noted Crew's suggestion that the destruction of the ovary by this disease "so altered the general metabolism of individuals that the conditions favorable to the differentiation and growth of spermatic tissue were created." Though he later twice refers to this "metabolic disturbance" Crew evidently does not consider this a final or sufficient description of the matter. He also attempts to apply another, and we believe demonstrably erroneous, conception. In the application of this hypothesis he apparently quite neglects the obvious metabolic change, though he earlier speaks for its existence in the case described, and though the present writer has formulated anew "the metabolic theory of sex," as noted above, and has presented much evidence of many kinds showing that changes in metabolic level are the *primary* source and cause of sex modification and control.

Crew sponsors the view that the ovary in process of destruction by disease is stimulated to a production of sex-cords late in life, and that these proliferations, precisely because of their appearing late in life instead of within the embryo, have a tendency toward the production of maleness. This hypothesis—with an attempt to introduce Goldschmidt's "timing mechanism"— seems wholly untenable in view of Allen's[11] recent work which indicates that even in the mammal (mouse) there occurs a cyclical proliferation of the germinal epithelium into

[10] Riddle, O., *Jour. Infect. Dis.*, 1921, *29*, 544.

[11] Allen, E., *Amer. Jour. Anat.*, 1923, *31*, 439.

the cortex of the adult ovary at each normal oestrous period. These data, as well as considerable amounts of earlier work, indicate that such proliferations normally occur late in life in the higher vertebrates, and that they nevertheless normally produce ovarian not testicular elements. Even if such a "timing mechanism" would account for the instances cited by Crew—and we are convinced that it fails to do so—it again wholly fails to apply to sex-reversals in the gamete stage where, by different agencies, the reversals are effected at the same stage and in either direction. It fails in still other cases.

The further suggestion that the *right* testis in the sex-transformed fowl arose from an "incompletely atrophied right" ovary, is wholly improbable in the case of the dove. We think it also improbable, and a wholly unnecessary assumption, in the case of the fowl; for primordial germ cells were originally received at this area and a temporary (essentially embryonic) right ovary was early formed there in contact with the peritoneum. That same peritoneal area and the immediately subjacent cells which actually persist would seem, from the data available, to afford sufficient point and material for the derivation of the newly formed testis in both the fowl and pigeon. The removal of the ovary, together with its influence in maintaining the conditions of its own functioning and of femininity, and the onset of a disease leading to the establishment of the specific condition—increased metabolism—favorable for male production, would seem to be the essentials required for the formation of testicular tissue from the peritoneum at the site of the embryonic ovary.

If the dove described here had died or been killed at any of several different times between the laying of the last egg and a year or two thereafter, we would then almost certainly have found an ovo-testis on the left side and a testis on the right; and also a greater or less predominance of ovary in the ovo-testis depending upon how soon the bird was killed after laying. Similarly, one or

another stage of transformation of the sexual ducts would have been found. Depending upon the stage attained at the time the bird happened to be killed, and the amount of latitude offered by an inadequate previous sexual history, this same bird could have been described as any one of several kinds of "hermaphrodite." It is a great merit of Crew's work, hardly second to his demonstration of a case of complete sex-reversal, that he has also made it clear (though by inference only does he refer to the point) that many at least of the "hermaphrodites" found in higher animals have a new meaning. The present case confirms and establishes the fact.

This new meaning the "hermaphrodites" derive from their proved relationship to the transformability or reversibility of a classic case of a chromosome-determined character. In view of the demonstrations described and discussed in this paper, and in earlier work, it can scarcely be contended that there are other chromosome-determined characters of organisms which are not transformable or reversible.

In the reversibility of characters on the one hand, and in the now obvious and unquestioned normal influence of the chromosomes on the other, biology nowadays presents the two sides of the problem of individual development. Who will venture that the plastic member of the pair is the less important in phyletic development—in evolution? Thus far genetics and cytology have each adopted the chromosomes as its own; but they bestow scarcely a limping gesture upon the facts of reversibility. The advancement of our knowledge of plasticity and controllability of hereditary characteristics does require other methods and aims than those now prevalent in genetics and cytology; but studies conducted in this newer field must unfailingly utilize the facts gathered from those two branches of science—and make a heavy call upon other branches of biology, physics and chemistry besides. The field of modifiability is not only the more alluring aspect of development—it promises results

of more practical importance. Though we may not hope to take from or give to the chromosomes of mankind, the temporary transformability—not a mere modifiability—of probably all alternative genes of every human being and of every organism is a scientific possibility which awaits only the work of the investigator.[12]

V

The complete reversal of sex from female to male in an adult ring dove has been described.

In this dove and in a similar case in the fowl earlier described by Crew the ovary was destroyed by tuberculosis. The relation of this disease to the establishment of an increased metabolism and of maleness is pointed out.

Many so-called hermaphrodites of higher forms are really stages of sex-reversal.

The demonstrated over-mastering of the sex-chromosome mechanism has wide and important applications in biology.

TABLE I

RECORD OF *St. risoria* NO. 16,580, 1914–1917 (AND OF MALE MATE)

♂ *St. risoria* (16,588) from Mr. Johnson 1/15/14.
♀ → ♂ *St. risoria* (16,580) from Mr. Johnson 1/15/14.

A1.	1/27	7.82 wt.	yolk, 1.880.
A2.	1/29	8.54 wt.	yolk, 2.135 = + 13.6 per cent. larger.
B.	2/17	(6.32) wt.	yolk, 1.940 (prematurely laid).
C1.	3/7	8.30 wt.	yolk, 1.810.
C2.	3/9	9.06 wt.	yolk, 2.080 = + 14.9 per cent.
D1.	3/21	7.55 wt.	yolk, 1.480.
D2.	3/23	9.27 wt.	yolk, 2.200 = + 48.7 per cent.
E1.	4/2	7.70 wt.	yolk, 1.500.
E2.	4/4	8.61 wt.	yolk, 1.700 = + 13.3 per cent.
F1.	4/13	8.41 wt.	yolk, 1.820.
F2.	4/15	10.45 wt.	yolk, 2.256 = + 24.0 per cent.

Incubated other eggs; hatched, deserted 5/5.

5/30/14—Incubated without laying eggs; eggs given, hatched, deserted 6/21.
7/28/14—Incubated without laying eggs; eggs given, hatched, raised.
10/24/14—Incubated without laying eggs; eggs given, removed, 11/16/14.

[12] This manuscript was written for publication in *Science*. It is hence a more condensed treatment of the subject than would otherwise have been given here.

Birds brought to new building February 1, 1915.
Feb., 1915, copulations frequent—but no eggs!

2/10/15—♂ 16,588 copulated as a ♂.
2/16/15—♂ 16,588 tail pulled out catching bird.
2/28/15—♀ 16,580 copulated as a ♂.

(New tail feathers of ♂ 16,588 only 3 cm long.)

3/ 4/15—♀ 16,580 copulated as a ♂.
3/26/15—♀ 16,580 copulated as a ♂.
3/27/15—♀ 16,580 copulated as a ♂ (at 12:15).
3/27/15—♂ 16,588 copulated as a ♂ (at 12:50).

April to September these birds often noted as willing to incubate eggs, without laying. Were used to incubate temporarily several pairs of eggs, and reared one set of young.

10/ 7/15—♀ 16,580 now "cooing as a male!"

1/15/16—Pair incubated without laying; eggs given, fed young 2/3 to 2/8.
2/20/16—Copulation observed but failed to learn which functioned as ♂.
3/ 2/16—16,588 "cooed" strongly as ♂, in attitude preliminary to mounting, but tamely concluded the performance by going to the seed pan, where he fell leisurely to eating.
3/25/16—Incubated without laying (to 4/12).

April 12 to May 28 pair wholly idle, removed to a pen with other inactive ring-doves.

♂ 16,588 dead 7/16/16. Autopsy: Considerably emaciated; lungs probably not normal but no tuberculosis; likewise none in spleen or liver; testes of rather small size—the right = 0.124 g (11.9 x 5.2 mm); the left = 0.104 g (12.1 x 4.5 mm).

♀ → ♂ 16,580 dead 12/29/17. Autopsy: Very tuberculous liver and spleen; the testes small; but not of the extremely small size usually associated with the most advanced tuberculosis; right testis, 0.030 g; the left, 0.035 g.

(There was no qualification whatever at autopsy, concerning the *maleness* of this bird; no suggestion of an ovary, which if present was certainly imbedded in the tuberculous mass involving spleen and liver. Since it was not realized at the hour of autopsy that this was the former female of the pair traces of an oviduct would also have been overlooked in minimizing the handling of this highly infected bird.)

SHORTER ARTICLES AND DISCUSSION

INHERITANCE OF PROTEROGYNY IN MAIZE

Most maize plants are proterandrous, the pollen being shed from three to five days before the first silks appear.

An exception to this general rule is found in a variety of popcorn imported from Spain in which pollen is first shed two or three days after the first silks emerge.[1] The uniformity with which the proterogynous habit was expressed in the plants of the original importation indicated that this condition would prove to be heritable. Three generations from self-pollinated proterogynous plants have been grown and the frequency distributions of the number of days from the appearance of the first silks to anthesis for the three years are remarkably uniform.

This uniform behavior made it desirable to test the inheritance of the proterogynous habit in hybrids with normal proterandrous maize. A hybrid was made with an inbred strain of Pawnee maize which had proved to be exceptionally vigorous.[2] The behavior of the F_1 with respect to the proterogynous habit was not measured other than to record that the plants were proterandrous by the usual number of days and were remarkably uniform.

The F_2 and both parents were planted and the number of days from planting to anthesis, and to the appearance of the first silks as well as the number of days from pollen to silk were recorded.

The parents behaved as in former generations. The proterogynous strain averaged $2.96 \pm .18$ days from silking to pollen while the proterandrous strain shed pollen $2.3 \pm .11$ days before the first silks appeared. No proterogynous plants were found in the proterandrous strain which with respect of this character was remarkably uniform. On the other hand the proterogynous strain as in former generations produced several proterandrous plants although the two parents did not overlap in this respect. In addition to the proterandrous plants and similar also to former generations, the proterogynous strain produced several

[1] Collins, G. N. A Variety of Maize with Silks Maturing Before the Tassels. U. S. D. A. Bur. of Plant Industry Circular 107, 11 p. Feb. 7, 1913.

[2] Collins, G. N. Intolerance of Maize to Self-fertilization. *Jour.* Wash. Acad. of Sciences. pp. 309–312, Vol. 9, No. 11, June 4, 1919.

plants that failed to extrude the anthers and never shed pollen.

The plants of the F_2 extended the range of proterandry by ten days, two plants shedding pollen twenty days before the first silks appeared, while one plant was proterogynous by a period of thirteen days. The mean of the F_2 population, however, was proterandrous by 4.45 ± .23 days, while the mean of the Pawnee parent was 2.30 ± .11 and that of the Granada was — 2.96 ± .18 days. Although the mean proterandry was greater in the F_2 than in the Pawnee parent the mode was almost exactly intermediate between that of the two parents, the mode of the proterogynous parent being at — 4 to — 5 days, that of the proterandrous parent at 7 to 8 days, and the F_2 at 1 to 4 days. The frequency distributions for the two parents and the F_2 are shown in Fig. 1, and the means are given in the following table:

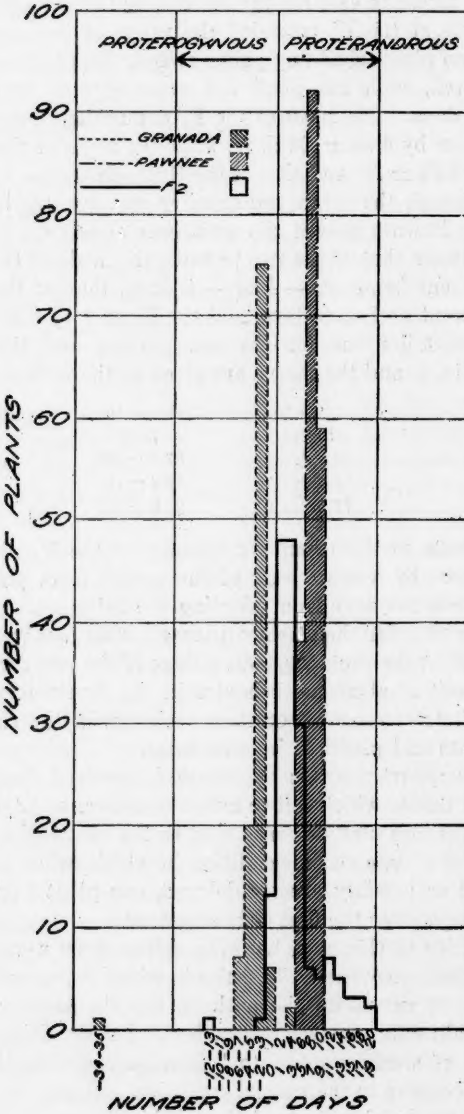
	Days to Pollen	Days to Silk	Days Pollen to Silk.
Granada	90.6 ± .22	87.6 ± .26	—2.96 ± .18
Pawnee	80.4 ± .17	82.5 ± .17	2.30 ± .11
F_2	77.5 ± .19	81.5 ± .24	4.45 ± .23

The increase in the mean proterandry of the F_2 plants was brought about by a shortening of the period from planting to anthesis, while the days from planting to silking was essentially the same as that for the Pawnee parent. This fact would seem to indicate that the proterogynous nature of the pop corn parent was the result of abnormal behavior in the development of the staminate inflorescence rather than a change in the relation of the staminate and pistillate inflorescences.

Further support for this hypothesis is received from the occurrence of plants which fail to extrude anthers and the proterogyny in this case may be considered as the result of a variable expression of a male sterile condition in which pollen formation is inhibited or possibly greatly delayed, one plant having shed pollen 35 days after the first silks appeared.

The sterility in this case, however, differs from a male sterile condition often encountered in maize in which the spikelets function normally, extruding the anthers, but the anthers of such plants contain only undeveloped pollen and never dehisce. This latter type of sterility seems to behave as a simple Mendelian character recessive to the normal condition and may be identical with that reported by Eyster,[3] though his illustrations and de-

[3] Eyster, Lewis A. Heritable Characters of Maize VII Male Sterile. *Jour. of Heredity*, Vol. XII, No. 3, pp. 138–141, March, 1921.


100
90
80
70
60
50
40
30
20
10
0
NUMBER OF PLANTS
PROTEROGYNOUS
PROTERANDROUS
GRANADA
PAWNEE
F2
-34 - -35
-12 - -13
-10 - -11
-8 - -9
-6 - -7
-4 - -5
-2 - -3
0 - -1
1 - 2
3 - 4
5 - 6
7 - 8
9 - 10
11 - 12
13 - 14
15 - 16
17 - 18
19 - 20
NUMBER OF DAYS

scription more nearly fit the sterile plants of the proterogynous Granada pop corn.

In the Granada strain, however, the percentage of sterile plants is much less than the expected 25, the observed percentage being 13.9 ± 1.8. This percentage of sterile plants, low from the standpoint of a simple Mendelian character, is encountered also in the F_2 population of the cross between the proterogynous and proterandrous varieties, the percentage of sterile plants in this population being 16.0 ± 1.73. The low percentage hardly can be the result of a high death rate for plants of this genetic constitution, an explanation which so often is applicable with other recessive characters but may be brought about through the interaction of modifying factors which tend to inhibit sterility.

In this connection it is interesting to observe that the percentage of sterile plants is essentially the same in the F_2 of the cross between Granada and Pawnee as it is in the Granada parent, indicating that if modifying factors for sterility are involved in the Granada strain the same factors are present also in the Pawnee variety.

The percentage of proterogynous plants in the F_2 eliminating those plants which failed to shed pollen is 8.7 ± 1.4 suggesting the 6.25 per cent. of a dihybrid character, but an inspection of the frequency distributions show that the nature of the inheritance is not so simple.

The proterogynous plants of the F_2 have a mean of but 1.47 as compared with the mean of 2.96 days for the proterogynous parent offering little support for the hypothesis that only two factors are involved in the expression of this character and that the proterogynous tendency has been recovered completely in this hybrid. In fact, from the behavior of the F_2 plants it would seem that an extreme condition of proterandry could be established with more certainty from this hybrid than could an extreme condition of proterogyny, though it is clear that the proterogynous tendency is inherited and can be transmitted through hybrids with the normal form.

The nature of the causes underlying the expression of the proterogynous condition are obscure. Photoperiodism, which plays such an important part in the development of the floral organs, does not seem to be an important factor in determining the relative maturity of the sexes in maize. While it had been possible by the use of an extremely short day to cause the development of pistillate flowers, or even apogamy with all the

intermediate stages, in inflorescences which under normal conditions would be entirely staminate, we have not produced artificially a condition approaching the sterility manifested in the proterogynous Granada strain.

Proterogyny in maize may be considered as a reversion to an ancestral condition since it is normal to Tripsacum, Euchlaena and Coix. It must be noted, however, that with the advancing season the inflorescences of Tripsacum change gradually from a proterogynous to a proterandrous condition, a change accompanied by an alteration in the ratio of staminate to pistillate spikelets, the late plants having a higher percentage of pistillate spikelets than the early ones. This behavior certainly would seem to indicate that the relative maturity of the sexes in this genus was subject to environmental influences and the phenomenon is strongly suggestive of photoperiodism.

No such behavior, however, has been found in Euchlaena and even under artificial long and short days if staminate spikelets are developed at all the inflorescences always are proterogynous. In this connection, however, it should be noted that the relative maturity of the two sexes might depend upon a particular combination of daylight and darkness, a combination which was not used in the experiments tried thus far.

The nature of the inheritance of proterogyny in the Granada-Pawnee hybrids is very similar to that encountered in crosses between maize and teosinte. In the teosinte-maize hybrid, however, the proterogynous condition is not recovered invariably, some hybrids producing only proterandrous plants.

In teosinte and teosinte-maize hybrids also no indications of a male sterile condition have been found, all plants shedding pollen even though extremely proterogynous.

Summary

Proterogyny, which is the normal condition in Tripsacum, Euchlaena and Coix, has been found to be normal also in a variety of maize from Spain. In hybrids with normal proterandrous maize the proterogynous condition behaves as a recessive character and the F_1 is proterandrous.

Proterogynous plants are recovered in the F_2, though in too few numbers for a simple Mendelian character. The frequency distribution of the F_2 plants of the maize hybrid is very similar to those obtained in teosinte-maize hybrids. From the occurrence of male sterile plants, and the character of the frequency distri-

bution, it seems probable that proterogyny in maize is the result of a variable expression of a male sterile condition, the variability being brought about through the interaction of modifying factors.

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OBSERVATIONS ON A NEW TYPE OF WINTER FEEDING GROUND FOR THE FRINGILLIDAE

While conducting some investigations of the animal microorganisms in the sprinkling filter of a sewage disposal plant at Bound Brook, New Jersey, the writer, during the months of December, January and February, had several times observed large flocks of birds apparently busily engaged in securing food from the surface stones of the filter bed, working rapidly between the periods of the activity of the sprays. A closer study of these birds and of the sort of food they were securing from the filter bed brought to light some new and interesting relationships.

At the Bound Brook Sewage-Disposal Plant, after the water from the incoming sewage has had its suspended materials partly removed in settling tanks, it is sprayed from a multitude of nozzles over a bed six feet in depth, composed of irregular basaltic stones, about the size of small eggs, to insure purification before it is allowed to drain off into a neighboring brook.

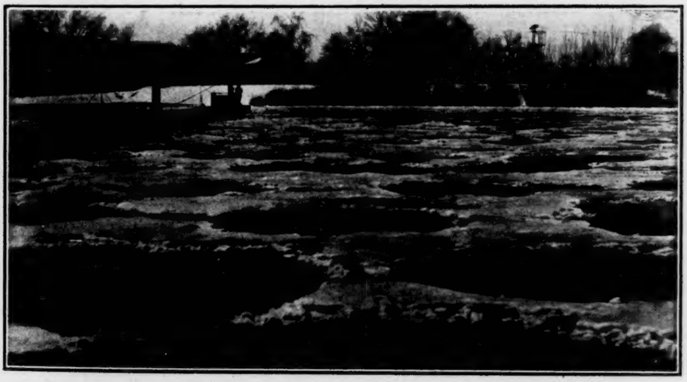

Fig. 1

A portion of the filter bed, showing the sprays in operation. In winter the beds are often covered with snow and ice except in the areas reached by the sprays

Fig. 1 shows approximately one third of the bed. On the stones over the surface of this bed there flourishes a rich greenish mat, composed of *Oscillatoria* and other algae, and underneath the stones, and continuing to the bottom of the bed there collects a heavy, slimy growth consisting of various fungi, with entangled bacteria in gelatinous matrix, cellulose débris, protozoa, nematode and annelid worms, tardigrades, rotifers and other minute forms. Near the surface of the bed there develop immense numbers[1] of moth flies (*Psychoda alternata*), the larvae and pupae of which are found together throughout the winter, just beneath or on the sides of the surface stones, together with many newly emerged adults (Figs. 2, 3 and 4). This transformation is continually taking place even during the very coldest months of winter. It was these forms that the birds observed were chiefly engaged in gathering. A few of the larger annelids found in the filter film (covering the stones), such as Pristina and Aeolosoma, are present near the surface, but usually underneath the surface of the film, and invisible.

The birds feeding on the filter bed were the tree sparrow (*Spizella monticola*), song sparrow (*Melospiza melodia*), junco (*Junco hyemalis*) and the goldfinch (*Astragalinus tristis*). These occurred in flocks of from 50 to 150 individuals, with the juncos and song sparrows the most numerous, and the tree sparrows and goldfinches in less numbers. At times there were two or more separate flocks feeding on different portions of the filter bed, making a total of some 300 or more individuals at work. From observations on the rapidity of feeding it was judged that, on an average, each bird secured one bit of food (doubtless one larva, pupa or adult *Psychoda* fly) every two seconds, making 30 individual organisms per minute for each bird, or 1,800 per hour. This would make a total of 270,000 organisms for a flock of 150 birds, or over half a million when the flocks totaled 300, as they sometimes did. And if 150 birds, at least, were at work on the beds during, let us say, four hours a day, the number of organisms consumed would reach 1,080,000.

The birds fed upon the filter bed during two-minute periods when the sprays were quiet, flying to other parts of the bed when

[1] The average number of *Psychoda* larvae, pupae and adults for ten stones from various portions of the surface of the filter bed taken during the months of January and February was 54. Just beneath these stones were almost solid masses of larvae, which were continually crawling towards the surface along the sides of the surface stones, and there pupating and emerging.

FIG. 2. Larvae of the *Psychoda* fly (× cir. 10). FIG. 3. Pupa of the same (× cir. 18). FIG. 4. Adult (× cir. 10).

the sprays over the portion where they were feeding began operation. Frequently, during the active period of the sprays they left the bed altogether and flew into nearby bushes and weed patches, to continue their feeding upon weed seeds. Not all the birds left the beds, however, even during the spraying. Some song sparrows and occasionally some juncos were seen hopping about under the sprays, avoiding the descending water-drops as best they could.

It is interesting to note that these birds, typical seed-eaters, neglected the weed patches, of which there were many close to two sides of the filter bed, in preference for the Psychoda larvae, pupae and adults. Within a stone's throw from the filter bed, on two sides, were patches of bushes and woodland wherein grew quantities of such weeds as the giant ragweed, smartweed, pigweed, moth mullein, evening primrose and others. An examination of these weeds showed that they were plentifully supplied with seeds. A microscopic examination of film from the surface of the filter bed revealed few or no weed seeds.

Of the birds seen on the filter bed the tree sparrow is probably the most exclusively seed-eating, seeds forming about ninety-eight per cent. of its food. Fifty per cent. of this is weed seed.[2] The junco is also largely a seed-eater, while the song sparrow feeds upon weed seeds to the extent of about fifty per cent. The goldfinch, while chiefly a seed-eater like the rest of the fringillids, has been seen, in winter, to consume large numbers of plant lice eggs. One stomach examined contained 2,210 eggs of the white birch aphid.[2]

The presence of an immensely rich supply of food in the shape of *Psychoda* larvae, pupae and adults, and the ease with which

[2] Forbush, E. H., "Useful Birds and Their Protection," 1905.

this can be secured in winter, has resulted in a considerable modification of the dietary of those birds feeding at the filter beds. Newcomers are attracted to the beds probably both by the sight of bare ground in the midst of a snow-covered landscape, and by the presence of flocks of birds of their own or of a congenial species.

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HELIX PISANA IN CALIFORNIA

Many years ago[1] Professor J. L. Howe published a detailed account of the Virginia colony of *Helix nemoralis,* showing that it had produced an extraordinary number of hitherto unrecorded band-variations. Another very variable species introduced from Europe is *Helix* (*Euparypha*) *pisana* Müller, which has become so great a pest at La Jolla, California, that strenuous measures have been taken to exterminate it. Thinking that the La Jolla colony might show some deviations from the usual type, I asked Mr. A. J. Basinger for specimens, and he has very kindly furnished an abundant supply. An analysis of this material shows that in form and texture it represents typical *H. pisana,* but varies in color and marking as follows:

(1) *pisana* proper, with numerous bands. 351 shells, of which more than 20 have the banding confined to the region just before the aperture.
(2) variety *bifrons* Moquin-Tandon, with the banding confined to the lower part of the shell, below the periphery. 122 shells.
(3) variety *alba* Shuttleworth. Whitish, tinged with ochreous, unbanded or with slight traces of bands. 213 shells.
(4) variety *subzonata* Bourguignat. With broad pale fulvous bands above and below the periphery, and often a more distinct basal band. 25 shells.
(5) variety *interrupta* Moquin-Tandon. With a very slender, more or less broken (punctiform) peripheral band, and usually some more or less interrupted banding below. Seven shells.
(6) variety *punctella* Moquin-Tandon. A more extreme form of the last, with series of dots in place of bands. Two shells.
(7) variety *sagittifera* Taylor, with arrowhead-like markings, but in our specimen they are confined to the region just before the aperture. One shell, not adult.

Although it is thus possible to catalogue seven named forms, the series is in fact a quite ordinary one, not showing any de-

[1] American Naturalist, XXXII, December, 1898.

parture from the condition observable in many European localities. While we lack experimental evidence, we may infer that the banding is due to at least two factors, a banding factor proper, and an activator of this factor. The latter may not operate early in the life of the snail, so that many shells are banded only toward the aperture. The variety *alba* probably lacks the activator. In variety *subzonata* groups of linear bands are fused and represented by pale reddish zones; apparently a modification of the banding factor. In *interrupta* and *punctella* we may suppose that the activator operates at regular intervals, how or why is not known. The *sagittifera* type is even more singular, the pigment forming foci on the mantle edge widening at intervals. It is evident that the species will repay experimental investigation.

The above list of varieties gives little idea of the range of variation of this snail, which has been figured by J. W. Taylor on two beautiful colored plates.[2] The small island of Porto Santo, in the Madeira group, produces *H. pisana* of much greater variety, as I have myself observed.[3] The variations seem to have little or nothing to do with environmental conditions, very diverse forms existing under the same environment. Taylor cites a case in which change of locality appears to have affected *H. pisana*, but it should be reinvestigated. The story is as follows:

> M. Mabille has also described its introduction in 1870 to the banks of the River Marne at Charenton, near Paris, as being due to a friend who, on his return home from travelling in the south of France, brought with him a large basketful of these snails for table use, but falling ill, the nurse, who attributed his malady to the snails, emptied the basket containing them upon the river bank, by the omnibus depot, where the environment being favorable, they prospered, but, according to Dr. Germain, have gradually become modified, as though at first all were fine, strong and distinctly banded shells, the great majority are now, though still of good size, of a delicate texture and a pure subtransparent white.

Nevertheless, in spite of its wide distribution and great variability, the species appears to have produced few distinct segregates. The British colonies, of which that at Tenby is the best known, do not show any special features; but it is at least possible that the snail has been introduced into Britain by human means within historic times. It has however been known as British since 1777.

[2] Monograph of the Land and Freshwater Mollusca of the British Isles. Part 19. (1912.)

[3] *Proc.* Malacological Society, XIV (1921), p. 196.

In France, Locard recognized five members of the *H. pisana* group: *H. pisana* Müll., *H. pisanella* Servain, *H. cuttati* Bourguignat, *H. carpiensis* Let. and Bourg., and *H. bertini* Bourguignat. Germain[4] does not hesitate to reduce all these to *H. pisana*, which is the only *Euparypha* described in his work.

In Syria, Morocco, etc., there are some distinct species and races of *Euparypha*. One of the most remarkable is the *H. ustulata* of Lowe,[5] confined to the Salvage or Selvage Islands, far out in the Atlantic. This is certainly a valid species. Unfortunately, it appears to be on the point of extinction. My friend Mr. A. C. de Noronha recently visited the Selvages, and informs me that whereas *H. ustulata* was formerly common, it now becomes rarer and rarer, perhaps owing to the lack of sufficient rain in recent years. He could not find a single living adult.

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University of Colorado

[4] Mollusques de la France et des Régions voisines. (1913.)

[5] This species is listed by Pilsbry as *H. macandrewiana* Pfeiffer. Lowe's name is the valid one, and is not preoccupied. The name *ustulata* Jay, 1839, was published under *Bulimus*, and refers to a color-variety of *Cochlostyla chrysalidiformis* Sowerby.